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Ecological Interaction Among Natural Enemies and its Consequences for Biological Control

Gary C. Chang

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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2000

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Robert T. Paine

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Date: August 17, 2000

University of Washington

Abstract

Ecological Interaction Among Natural Enemies and its Consequences for Biological Control

Gary C. Chang

Chairperson of the Supervisory Committee:
Professor emeritus Robert T. Paine
Zoology

One goal in pest control is to develop methods that suppress pests without harming other organisms. With this in mind, an ideal method would be to augment non-target organisms to control a pest. This can be accomplished by augmenting natural enemies. However, augmentative biological control is often difficult and complicated. For example, when several species of natural enemies attack the same pest population, their action may combine to improve biocontrol. On the other hand, examples also exist of natural enemies disrupting each other and decreasing pest control. I review recent literature on arthropod systems and find more cases of improved biocontrol with multiple natural enemy species (Chapter 1). The behavior of individual arthropods can sometimes explain whether different natural enemies are compatible for pest control. I present empirical data on the foraging behaviors of several natural enemies in western

Washington pea fields (Chapter 2). These natural enemies consume the primary pest in the system, the pea aphid (*Acyrthosiphon pisum*), but they also attack each other ("intraguild predation"). The intraguild predators include lacewings (*Chrysoperla carnea*) and ladybird beetles (Coccinellidae), while the intraguild prey include syrphid flies (Syrphidae) and parasitoid wasps (*Aphidius* spp.). I could not find a statistically significant difference in encounter rate with pea aphids of intraguild predators compared to intraguild prey. If encounter rates reflect the exploitative ability of the natural enemies in the system, then theory predicts that intraguild predation will not disrupt biocontrol. Field experimentation suggests that intraguild predation does not disrupt biocontrol of the pea aphid (Chapter 3). I conducted several field experiments in which I augmented populations of lacewings or ladybird beetles. If lacewings or ladybird beetles disrupt biocontrol, then pea aphid populations should increase in predator-treated plots. Instead, in four out of five experiments, predator augmentation was associated with statistically insignificant decreases in pea aphid populations. Thus, while intraguild predation does not disrupt biological control of the pea aphid, predator augmentation did not substantially improve aphid control. The effect of predator augmentation was dwarfed by unmanipulated large-scale factors such as weather and site location.

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Acknowledgements

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Dedicated to the memory of my mother, Lillian Chang

Introduction

The organisms we consider pests present a management dilemma. On one hand, we can do nothing and tolerate the damage that pests inflict upon human health, economics and quality of life. On the other hand, pest control actions often have undesirable effects on non-pest species. While no easy resolution exists to the pest dilemma, biological control is one potential option. In biocontrol, beneficial non-target organisms are used as agents to control a pest. Biocontrol by augmenting and/or conserving native species that already reside in an area is particularly appealing. Natural enemies of pests such as predators, parasites, and diseases are often employed as biocontrol agents. However, natural enemies are not always specific enemies of just a target pest. The non-target effects of intended biocontrol agents can make control efforts counterproductive. In some cases, biocontrol agents can interfere with each other and increase, rather than decrease, densities of the target pest (Rosenheim et al. 1993). Intraguild predation (the consumption of a potential competitor; Polis et al. 1989) is an interaction that can lead to the disruption of biological control. I find the behavior of intraguild predation intrinsically interesting. I am also interested in it because of its potential implications for biological control programs, and therefore sustainable agriculture.

Much of the conceptual foundation for my work is found in the reviews by Polis et al. (1989), Polis and Holt (1992), Rosenheim et al. (1995), Rosenheim (1998) and Sih et al. (1998). The following chapters address intraguild predation and other potential complications in pest control situations where several natural enemies attack the same pest. Chapter 1 consists of a literature review of studies of multiple species as biocontrol agents. I found 112 papers in which multiple species of natural enemies were studied as biocontrol agents. While most of the papers involved 15 or fewer species of natural enemies, one involved 493 biocontrol agents (Settle et al. 1996). Although agricultural ecosystems may be depauperate when compared to native habitats (Valladares and Salvo 1999), they will still often contain several interacting species.

The consequences for pest populations attacked by two natural enemy species range from disruption to synergism (Ferguson and Stiling 1996). Synergism describes the case in which the two enemy species have a greater joint effect on the shared prey than the sum of the two species effects in isolation (Losey and Denno 1998) and is the most desirable outcome for biocontrol workers. Disruption occurs when the prey population is higher in the presence of both natural enemies than in the presence of either one of them individually (Rosenheim et al. 1993). Disruption is clearly unacceptable among biocontrol agents. Additive effects are seen when the joint effects of two biocontrol agents are the sum of their individual effects (Chang 1996) and antagonism describes joint effects that are less than additive but still greater than either natural enemy's individual impact.

Natural enemy interactions may also increase or decrease the population densities of the members of the guild (Root 1967) of natural enemies. Effects on the natural enemy guild are worth considering because not all natural enemies used in biocontrol programs are originally found in the system. The classical and most frequently used mode of biocontrol involves importing an exotic natural enemy to control an exotic pest species. A classical biocontrol agent may replace native natural enemies without decreasing the population density of the target pest (Elliott et al. 1996). The loss of native biodiversity without improved pest control is unsatisfactory from a conservation biology standpoint. Similarly, antagonism between classical and incumbent biocontrol agents may be unacceptable, while antagonism (but not disruption) between two incumbent natural enemies in an augmentative or conservation biocontrol program can be tolerated.

In most of the 112 papers in the literature review, enhancing the natural enemy guild was thought to improve biocontrol. However, it is important to understand why natural enemies can sometimes disrupt each other. Disruption and other population-level outcomes can often be explained by mechanisms such as foraging behavior of the natural enemies. For example, the extent that two natural enemies overlap in space and time between foraging can influence how likely they are to come into contact with each other. If two natural enemy species are likely to come into contact with each other, then they may eat one another in an interaction called intraguild predation (IGP; Polis et al. 1989). The occurrence of IGP can contribute to, but does not insure, disruption. As often as not, including an IG predator in a system with another natural enemy can still improve biocontrol (Rosenheim et al. 1995). Still, when disruption is seen between two natural enemies, it is often due to IGP. Several general mathematical models predict the conditions under which IGP will disrupt biocontrol (Hassell 1978, Polis et al. 1989, Polis and Holt 1992, Schreiber and Gutierrez 1998). Two conditions stand out that produce disruption. One is when IG victims are superior exploiters of the pest than IG predators. The other is when IG predators take IG victims in preference to pests.

I examined IGP and biocontrol in western Washington pea fields, where pea aphids are the primary pest (Chapter 2). At least 12 other herbivorous arthropods and 40 of their natural enemies have been found in the pea field system (Appendix C). To collect behavioral data on the various natural enemies in pea fields, I followed individual natural enemies for 15 minutes or until lost. I recorded where individuals foraged (parts of the pea plants and off-plant areas), what they encountered, and the outcomes of encounters. I recorded a cumulative total of 79 hours among 26 taxa and witnessed 156 encounters. Seventy-nine of the 156 encounters resulted in a feeding event. Fifty-six encounters involved pea aphids as food items, while 6 involved natural enemies as food. These proportions do not differ significantly from the proportions of individual pea aphids and natural enemies in the field. Interestingly, the overlap among natural enemies with each other was greater than with pea aphids. Therefore, the proportionate kill rate suggests that natural enemies have behaviors or other traits that allow them to avoid or escape each other better than pea aphids can.

To summarize the behavioral perspective on impact of IGP on biocontrol here, I concentrate on a few key species. Two important groups of IG victims are parasitoids and syrphid flies. Two IG predator taxa are lacewings and various ladybird beetles. Lacewings were seen consuming dead aphids that contained developing parasitoids (mummies). Ladybird beetles were seen consuming mummies and larval syrphid flies. Lacewings, ladybird beetles, parasitoids, and syrphid larvae were all among the natural enemies seen attacking pea aphids. As mentioned above, the natural enemies took their prey in proportion to the abundance of different prey types. The other key comparison of exploitative abilities of the different natural enemies can be made by contrasting their pea aphid kill rates. The kill rates of lacewings, ladybird beetles, parasitoids and syrphids did not significantly differ from each other. Although models predict that the long-term coexistence of IG predators and IG victims that have similar exploitative abilities is unlikely, the recent association of much of the pea field community may explain why the IG predators have not excluded the IG victims. Furthermore, peas grow for only a few months, so the coexistence of the arthropod species found on them may depend on habitats other than peas.

With the behavioral data described above, one can predict that the augmentation of IG predators should not disrupt biocontrol in pea fields. Population-level observations and experiments were conducted simultaneously with the behavioral work (Chapter 3). The experiments were primarily designed to answer the question of whether augmenting confirmed IG predators would disrupt biocontrol by incumbent (also called "resident") natural enemies in an open field setting. Observations were made that to assess the level of impact that incumbent enemies had on pea aphid population densities and whether incumbents were likely to limit their net impact by IGP.

Due to differences among years and between sites, I conducted essentially five experiments. These were in Fife (WA) in 1998 and 1999 and Sumner (WA) in 1997 - 1999. In each experiment, several plots were located within the same field but separated by several meters from each other. Some plots were randomly chosen for predator augmentation while other plots acted as controls. Plots were periodically sampled through each growing season by randomly selecting individual plants, measuring them and surveying every organism on them. Logistical problems altered the experimental design. For example, in 1997 and 1998, I augmented lacewing larvae in treatment plots. However, the source lacewing colony collapsed in 1998, which is why I augmented predators in 1999 with tethered adult ladybird beetles.

Observations suggest that resident natural enemies have the potential to impact pea aphid populations. Two groups of natural enemies, parasitoids and fungi, leave physical evidence of the aphid mortality that they cause (mummies and cadavers, respectively). The densities of mummies and cadavers can be compared to the density of living pea aphids as a crude measure of natural enemy impact. The highest ratio of cadavers and mummies to living aphids was 0.53 in early 1997 at the Sumner site. In other words, roughly one third of aphids seen in that sample had been killed by either a parasitoid or fungus. However, visual inspection of population sizes over the seasons suggest that resident natural enemies rarely, if ever, cause declines in pea aphid populations. Instead, natural enemies may reduce the population growth rate of aphids, while declining plant resources eventually cause aphid declines.

If augmented IG predators disrupt resident natural enemies, then pea aphid densities should be higher in treated plots than in controls. In four of the five experiments, the opposite occurred, that is, plots in which lacewing and ladybird beetles were augmented had lower pea aphid populations than controls. While the difference was not statistically significant, it still indicates that the augmented predators did not disrupt biocontrol. Predator augmentation actually had little detectable effect on the populations of any of the species in the experiments. Although predator augmentation did not appear to affect pea aphid density, it may have affected pea aphid distribution within plots. In 1999, aphids were more evenly distributed on plants in treated plots.

Finally, IGP occurs among resident natural enemies, but it does not appear to substantially hinder biocontrol. Cadavers are closely correlated with parasitoids and ladybird beetles at multiple spatial scales, even when the influence of pea aphid density is accounted for by partial correlation. Ladybird beetles do consume cadavers (Chapter 2), but often only partially (Pell et al. 1997, Roy et al. 1998). Uneaten spores can be transported by beetles, so the fungal disease may be spread more widely among aphids through the action of ladybird beetles. Therefore, the net effect of ladybird beetles and fungi on pea aphid populations is not clear. In summary, low natural enemy density or effectiveness, rather than IGP, is probably the major limit on the effectiveness of biocontrol in pea fields.

Unmanipulated large-scale influences related to year and site differed among the experiments. Some of the idiosyncrasies of each experiment are related weather and landscape. For example, 1998 was unusually hot and dry, and was the only year in which substantial numbers of hunting wasps were observed attacking aphids. The next year, the summer was cooler and wetter than usual, and fungi became extremely abundant – but only at the Fife site. The Fife site, which is located in a mix of light industrial and agricultural zones, had generally lower densities of all arthropods except spiders. The large-scale influences produced major differences in the arthropod community that dwarfed the effect of the augmentation treatments. Thus, a mismatch occurs between the important influences on the study system and the primary question under study. I try to reconcile the mismatch with Chapter 4, which discusses some future directions inspired by this study.

Future directions for work relating IGP to agroecosystems may include both modeling and empirical efforts. Simulation models will require empirical work in order to estimate parameters. Another key question that requires empirical attention is whether a given natural enemy has mostly disruptive interactions with natural enemies in agroecosystems that have numerous natural enemy species. In other words, if an IG predator disrupts one other enemy, is it also likely to disrupt other natural enemy species, or will the disruptive interaction be "negated" by additive or synergistic interactions with other species?

Directions for practical work to improve biocontrol in peas include improving the practicality of augmentation and identifying habitat modifications that encourage natural enemies. Once again, multiple species will have to be considered. A problem could arise if habitat modifications that favor one natural enemy harm a different natural enemy. Intraguild interactions may also produce unexpected consequences for habitat modifications in and around biological control settings.

Chapter 1

Interactions and consequences of multiple species for biological control

Introduction

When many plants of a single type grow together in an area, they are thought to increase in "apparency" (Root 1973, Feeny 1976) and suffer more attacks from herbivorous insects. Because much modern agriculture uses such crop monocultures, many methods for reducing herbivore populations have been developed, from increasingly sophisticated chemical attacks on pests to the development of genetically-modified resistant crops. Both of these approaches can have negative environmental consequences, as noted by the public and many environmentalists. A traditional "organic" solution has been to develop natural enemies of the pests as control agents (Altieri 1995, Lewis et al. 1997). The use of native species for biological control has an additional intrinsic appeal because some of the system's biodiversity is maintained (Ehler 1998). However, the interactions between biological control species, many of which are generalist predators, may have consequences for pest control that must be understood. The fundamental biological question is whether attacks on pest species by a complex of predators will be additive, and therefore beneficial to the crop, or whether relationships within the guild of natural enemies will be self-inhibitory, and therefore negate their potential impact (Rosenheim 1998).

Myers et al. (1989) provocatively asked "How many insect species are necessary for the biological control of insects?" They found that in some cases, just one species is credited with successful biocontrol, while in other cases, several species are needed. This suggests a new question: "what determines whether multiple species produce better biocontrol than a single species?" Recent work emphasizes mechanisms such as spatial and temporal overlap in foraging behavior (Losey and Denno 1999) and propensity for interference. (Rosenheim et al. 1999, Schellhorn and Andow 1999a).

Before discussing the biology of multispecies interactions, it is necessary to consider how to evaluate biocontrol. The consequences of having multiple natural enemy species in a system can be examined from several perspectives. To the grower, the question is often reduced to whether multiple species of biocontrol agents will increase net profit or crop yield. However, relatively few biocontrol studies are conducted on a scale that allows economic assessment (but see Tisdell 1990, Gutierrez et al. 1999) or yield assessment (but see Snyder and Wise 1999). Instead, researchers often make the reasonable assumption that decreasing the number of pests attacking the crop will improve crop production (Bellows and Van Driesche 1999, Luck et al. 1999). Therefore, the effects of multiple biocontrol species may be gauged at the level of pest populations or mortality. The possibilities for the simplest such case, when two natural enemies act together, has been schematized by Ferguson and Stiling (1996). A similar graph can be generated for the augmentation or introduction of a natural enemy into a community where other natural enemies are already present (Figure 1.1).

In the context of biological control, synergism between different natural enemies is the most desirable outcome. However, it is important to remember that additive effects and even slight antagonism can potentially improve biocontrol over single-species conditions. When the combined mortality due to multiple species of biocontrol agents drops below the mortality inflicted by a single agent, or no control agent, then biocontrol has been disrupted.

The preceding view of multiple species for biological control provides a starting point for assessment, but a more complete picture includes a comparison of the interspecific and intraspecific interactions of natural enemies. This can be thought of in terms of prey populations or mortality (Figure 1.1), as well as in terms of predator abundance and community composition. For example, incumbent species of natural enemies may prevent the establishment of an introduced natural enemy species (Ehler and Hall 1982). However, assuming that a natural enemy species is successfully introduced or augmented in a system, several outcomes are possible at the level of the natural enemy guild attacking the prey (Figure 1.2).

Inhibition at the level of the natural enemy guild does not necessarily result in antagonistic effects at the level of prey populations. Similarly, what I call enhancement of the natural enemy guild does not necessarily improve pest control. This is because of the possibility that individuals of different species may have very different per capita effects on a prey population (Paine 1992), and interactions within the guild may change the strength of per capita effects (Fagan and Hurd 1994). Despite the difficulty in connecting responses of the natural enemy guild to pest populations, it is appropriate to examine the impacts of natural enemies on other members of their guild because of the recent and growing amount of attention being given to the negative environmental impacts of introduced, or "classical," biocontrol agents (Howarth 1991, Lockwood

1993, Nafus 1993, U. S. Congress 1995, Secord and Kareiva 1996, Schultz and Chang 1998, Strong and Pemberton 2000). While I will often discuss results in terms of changes in pest populations, other criteria will certainly influence whether or not a biocontrol effort should be considered successful.

Myers et al. (1989) reviewed papers that reported successful instances of classical biocontrol published prior to 1979. They tallied 15 pests that had been successfully managed by multiple species of biocontrol agents, versus 24 pests for which successful control was attributed to a single agent (usually out of a complex of natural enemies). However, of these 24 pests, control was not always by the same agent in different localities. For example, *Aspidiotus destructor* (an armored scale insect), was controlled by a *Cryptognatha nodiceps* (a ladybird beetle) on Fiji, *Aspidiotiphagus citrinus* (a parasitoid wasp) in Indonesia, *Rhizobius puchellus* (another ladybird beetle) on New Hebrides, and *Comperiella nodiceps* (another parasitoid wasp) in Principe. Thus, on a site-by-site basis (the perspective more likely to be useful to individual farmers), 35 examples were found where a single biocontrol species was given credit for controlling a pest. On the other hand, if pest management is considered on a global basis, then a total of 20 pests could be interpreted as being controlled by multiple species of natural enemies.

Myers et al. (1989) suggested that natural enemies that are rare where a pest is endemic might make the best classical biocontrol agents. They also suggested that high fecundity parasitoids might be kept at low numbers by competitors or hyperparasitoids (species that parasitize the primary parasitoid) in the area of endemism. The potential for hyperparasitoids to disrupt pest regulation has long been known (Wardle and Buckle 1923, Sweetman 1936, Hassell 1978). The evidence for competition limiting the effectiveness of biocontrol agents has been less clear (therefore igniting some heated debate: Ehler and Hall 1982, Ehler and Hall 1984, Keller 1984). The utility of the Myers et al. (1989) suggestion depends critically on intimate and local biological detail: recent studies have paid closer attention to the mechanisms by which different species of natural enemies interact, and thereby directly or indirectly influence the degree of pest control achieved in a system.

A sample of the literature on single versus multiple species for biological control

Although researchers and practitioners of biological control have recognized that some combinations of natural enemy species have the potential to enhance while others may undermine biocontrol (Myers et al. 1989), it is difficult to recognize the conditions that lead to improved biocontrol with additional natural enemy species. In this chapter, I sample the biocontrol and ecological literature to address the following three questions:

1. While agroecosystems are not as diverse as some other ecosystems, how many contain multiple species of potential biological control agents?
2. Does the use of multiple biological control agents produce a variety of pest control outcomes?
3. Can understanding the different mechanisms by which biological control agents interact help explain the variety of results obtained?

I have limited this review to articles describing biological control by natural enemies in pest arthropod systems. Two sets of articles are included in this review. The first set of publications (Appendix A) was assembled through a traditional selective perusal of the literature. The second set (Appendix B) was collected using a repeatable protocol in an attempt to obtain a representative and unbiased, yet manageable group of articles to analyze quantitatively. For the quantitative review, I have chosen to concentrate on recent publications in the journals *Environmental Entomology* and *Biological Control.* These two journals are widely available in North America and frequently publish articles on arthropod biocontrol by natural enemies. I examined every article published in these two journals between January 1998 and October 1999. Of these, 91 explicitly describe arthropod biocontrol systems in which multiple species of natural enemies are considered in the study (Appendix B).

The numbers of natural enemy species found in the selective and quantitative reviews combined (Appendices A and B) ranges from 2 (many studies) to a high of 493 (Settle et al. 1996). Over 70 different pest species were investigated in these studies.

Five of the studies (roughly 5%) compare multiple biocontrol agents independently of each other and declare a single best species as the most promising biocontrol agent (Figure 1.3). This suggests that the authors of those studies would recommend focusing rearing and augmentation resources on a single species rather than distributing efforts among multiple species for biocontrol. However, logistical rather than biological reasons may also impact such a decision (see below). Conversely, many studies (46) consider a guild of natural enemies rather than singling out particular species for attention, which may suggest that these workers would promote augmentation efforts that the abundance of the guild rather the abundance of just one species. Forty, or 44% of the studies in Appendix B explicitly considered the compatibility of different species for biocontrol.

Various methods and measurements of effect were used to address the compatibility of multiple species for biocontrol. A "vote count" reveals 21 studies that recommend increasing the number of species of natural enemies for biocontrol versus 4 recommending against using more natural enemy species (Figure 1.4). Fifteen studies did not explicitly recommend for or against multiple species of natural enemies for biocontrol. The studies in Appendix A also tend to favor more species for biocontrol, but to a lesser degree (11 pro, 7 con, and 3 that abstained from comment or found arguments for both sides).

The degree of compatibility among different biocontrol agents could be explained with several underlying mechanisms. These can be roughly grouped into 6 categories: 1) interference competition, including intraguild predation, 2) exploitative competition, 3) retreat after encounters, 4) habitat partitioning, including spatially, temporally, and by preferred host stage, 5) mutualisms such as predators vectoring pathogens, and 6) indirect effects. I will discuss each of these in greater detail below.

Practical constraints and considerations

It is difficult to interpret some of the studies in the sample because they describe rather than prescribe. Of course, this is not a short-coming of these studies, because biocontrol programs are often constrained. These constraints will depend on the type of biocontrol program and the stage that it is in. For example, survey studies are an invaluable first step in most biocontrol programs. The goal of most surveys is to identify the natural enemies that attack a pest in a particular area. Often, surveys will find multiple species of biocontrol or potential biocontrol agents and I have included them among those studies that examine guilds of biocontrol agents. However, it is often outside of the scope of a survey to identify the most promising agents even if some stand out above the others.

Other studies may be constrained by additional practical aspects of biological control. Studies that pick one out of several potential agents may indicate that the authors hold the opinion that multiple species could disrupt biocontrol. However, it may also reflect limited resources in a biocontrol program. For example, in a classical biocontrol program, prospective biocontrol agents of an introduced pest are selected overseas, often from a pool of many natural enemies. These species may differ in what they require to be reared successfully. Thus, given finite resources (such as growth chambers and incubators), only a few can be chosen for mass rearing efforts (Waage 1990).

In contrast, efforts to manipulate natural enemies by habitat modification, for example by intercropping or plant variety selection, may not permit much selectivity in the species that respond to the modification. A habitat modification that augmented multiple natural enemies was performed in several of the studies in Appendix B (Anderson and Yeargan 1998, Bigger and Chaney 1998, French et al. 1998, Geervliet et al. 1998, Smitley et al. 1998, Degooyer et al. 1999, James et al. 1999, Nabli et al. 1999, Prasifka et al. 1999, Rothwell and Smitley 1999, Roy et al. 1999, Wilson-Rummenie et al. 1999).

Occasionally, pests arrive in areas where they are completely free of natural enemies (for example, *Paraleyrodes minei* in California, see Bellows et al. 1998). However, the presence of incumbent natural enemies in many situations may in fact render moot the question of single versus multiple biocontrol agents. Still, in these situations, the question of how biocontrol agents interact remains important for understanding why biocontrol efforts succeed, fail, or vary by site (Rosenheim et al. 1995). Certainly, multiple species of classical biological control agents are often available for release against the same pest (Myers et al. 1989), and habitat modification can sometimes augment certain natural enemies more than others (Bottrell et al. 1998). Thus, the interactions between natural enemies and the consequences of those interactions will often need to be examined to optimize biological control in those situations. Fortunately (for those who use biocontrol), some studies have been specifically designed to compare pest control achieved with different numbers of species as biocontrol agents. To understand the mechanisms and considerations that influenced some of these studies, I will discuss their design and findings in detail.

Methodological considerations

Both experiments and observational studies are included in the appendices. I do not believe that any single approach to studying multi-species interactions can or should be declared as "the best." This is particularly true when considering the fact that biocontrol practitioners will not always have the luxury of choosing experimentally tractable systems to work in. Thus, it is for heuristic reasons that I devote the most space to discussing two-way factorial experiments over single-factor experiments and detailed observational studies.

The two-way factorial design (figure 1.5) is a straightforward experimental design that can be used to study the consequences of interactions between different natural enemies for biocontrol. The baseline experimental design of figure 1.5 has appeared occasionally in the biocontrol literature, often with additional treatments added to it (Appendices A and B). Prey mortality, population size, and/or population growth rate may be measured as dependent variables. The two-way design serves as a convenient starting point for framing questions about the interactions of multiple species of biocontrol agents. It is important to remember that behavioral data are useful in interpreting the different outcomes that have been obtained in population-level factorial experiments. Furthermore, the baseline design is limited in its ability to address intra- versus interspecific interactions among natural enemies without additional natural enemy density treatments. Also, many systems contain more than two biocontrol agents, and a factorial approach in those systems would be practically impossible. For example, a completely factorial approach to the rice agroecosystem studied by Settle et al. (1996) would require a total of $493^2 = 243{,}049$ predator treatments, not including replication.

Studies in these systems have been designed in a variety of ways, ranging from experiments that manipulate the entire guild of natural enemies to experiments that manipulate only a single biocontrol agent, to strict observational studies. Observational studies include comparisons of the community structure before and after the establishment of an introduced biocontrol agent, and detailed observations of the foraging behavior of particular natural enemy species.

The worst case for biocontrol: disruption

When the interaction between two natural enemy species results in a pest population that is higher than that seen when only one natural enemy species is present, this is disruption of biocontrol. In the most extreme case, the pest population is higher than when any single natural enemy is present. Rosenheim and his collaborators have highlighted disruption as a result from biocontrol agents eating each other instead of the pest (Rosenheim et al. 1993, Rosenheim 1998). This type of interaction has been dubbed "intraguild predation" (IGP) because it involves the consumption of a species that uses a similar resource (Polis et al. 1989). IGP is a direct interaction with intuitive short-term consequences: the loss of individual intraguild prey from the system.

Rosenheim's (1998) selective review of the literature found six or seven experimental disruptions of arthropod biocontrol due to IGP in interactions of parasitoids with predators and predators with other predators. One of these was

Rosenheim et al.'s (1993) stimulating study of IGP in California cotton involved a green lacewing, *Chrysoperla carnea*, and several hemipterans as predators of the cotton aphid *Aphis gossypii*. In a series of experiments conducted in field enclosures, these predators were tested singly and in various combinations to determine their impacts on *A. gossypii*. Only the treatment of lacewings alone caused negative per capita aphid growth over the 7-8 day duration of the longest experiment. Each of the three species of hemipterans tested singly decreased per capita aphid growth. When lacewings and hemipterans were combined, per capita aphid growth values fell between those obtained from the single biocontrol agent conditions. This disruption of biocontrol was due to IGP on lacewings by the hemipterans.

The use of field enclosures in Rosenheim et al.'s (1993) study left it vulnerable to criticism that it distorted the foraging behavior of the predators involved. Therefore, Rosenheim et al. (1999) directly observed foraging neonate lacewings to establish that they are vulnerable to IGP from hemipterans. Indeed, in a cumulative 448.6 hours of lacewing observations, 9 attacks on lacewings (involving 5 hemipteran species) were witnessed, permitting them to discount the view that IGP disruption was an artifact of the enclosures used in the 1993 study. It is worth noting the extensive amount of time required to collect the behavioral data, exceeding two days of cumulative observation for each event.

Diminishing returns: antagonism without disruption

Even if IGP is found, the level of pest control might still improve, as illustrated by the case of the aphid biocontrol agents *Diaeretiella rapae* and *Metasyrphus corollae* (Kindlmann and Ruzicka 1992). *D. rapae* is a typical parasitoid that lays its eggs inside aphids. As the immature parasitoid starts developing within the aphid, it causes the cuticle to harden. The aphid eventually dies and turns into a mummy that houses the close-to-mature parasitoid. Mummies are visually distinct from healthy aphids due to their thickened cuticles.

M. corollae is a syrphid fly that is predacious as a larvae. However, its maggot mouthparts are relatively undeveloped (when compared to the mandibles of other aphid predators such as lacewing larvae or even ladybird beetles). Therefore, *M. corollae* shows a pronounced preference for prey with thin cuticles (Ruzicka 1976). When both unparasitized aphids and aphids that have been parasitized by *D. rapae* are present, the healthy aphids are eaten out of proportion to their abundance (Kindlmann and Ruzicka 1992). Some IGP on parasitized aphids still occurs, so the combined effect of the two natural enemies is not perfectly additive, but still greater than the number of aphids when *D. rapae* is the only biocontrol agent. A drawback of this study is that it did not include a treatment of *M. corollae* acting alone on aphids, and so cannot address the effect of *D. rapae* on *M. corollae.*

Thus, from a strictly pest management perspective, if *D. rapae* were the only aphid predators in a system, no harm would be done by releasing *M. corollae*. However, from an economic standpoint, this may represent a case of diminishing returns from an investment in biocontrol. An additional concern from a conservation standpoint is the possibility of a introduced biocontrol agent displacing endemic guild members. This may be happening with the seven-spotted ladybird beetle, *Coccinella septempunctata*, which has been introduced to North America. Elliott et al. (1996) monitored the ladybird beetles in agricultural fields in South Dakota for 13 years prior to and 5 years following the establishment of *C. septempunctata*. The arrival of *C. septempunctata* was correlated with a decline in the abundance of native coccinellids so that the total abundance of all coccinellids did not change with the insertion of *C. septempunctata* into the guild. Several separate studies (Evans 1991, Evans and England 1996, Obrycki et al. 1998) have shown that for certain pests, *C. septempunctata* does not improve biocontrol. Hypothetically, the effect of *C. septempunctata* may be a loss of native coccinellid diversity without a change in pest control efficiency. Such a result is unsatisfactory from a conservation biology perspective, and indicates a trade-off that would make any antagonism in a classical biocontrol programs undesirable.

On the other hand, augmentative biocontrol programs employ strategies that boost the populations of incumbent biocontrol agents. Antagonism between indigenous biocontrol agents is tolerable as long as it does not lead to disruption. For example, the practice of polyculture can enhance populations of multiple biocontrol agents (Andow 1991, Altieri 1999). Antagonism between these biocontrol agents is acceptable as long as it does not increase pest populations.

A null hypothesis: additive effects

Additive effects between biocontrol agents represent a desired improvement over antagonism. In certain ways, additivity may be the most intuitive result of multiple natural enemies acting on the same prey, because the mortality from natural enemy A is simply added to the mortality from natural enemy B. In statistical terms, when an ANOVA is used to analyze the data gathered from a factorial-design experiment (i.e. figure 1.5), under certain conditions, an additive effect of having the two predators together is the null hypothesis (Wilbur and Fauth 1990).

Unlike some other null hypotheses, the additivity of natural enemies is not just the trivial expectation based on chance. Instead, like antagonism and synergism, additivity is produced by the behaviors of the natural enemies. It may be the case that two randomly foraging species may have additive effects when combined, but it is also the case that differences in their foraging patterns can produce additivity. For example, when Sengonca and Frings (1985) studied the interactions of *C. septempunctata* and *Chrysoperla carnea* (a green lacewing) in petri dishes, they concluded that interference and IGP might limit the efficacy of these two predators. However, when I studied the larvae of *C. septempunctata* and a North American green lacewing, *Chrysoperla plorabunda*, on individual caged host plants, their joint effect was additive on *Aphis fabae* (the bean aphid) populations (Chang 1996). I explained this contrasting result by the fact that the host plant provided different areas, such as stems, axils, leaf surfaces and edges, that the two predators differently preferred. In short, differences in the foraging behaviors of the two biocontrol agents mitigated IGP and allowed an additive result.

The best case for biocontrol: synergism

Synergism between biocontrol agents produces better pest suppression than is found in the case of additivity, and is clearly the most desired result from a biocontrol perspective. However, synergism seems difficult to document. Losey and Denno (1998) have presented the definitive example of synergism between predatory insects in an agroecosystem. They studied the pea aphid, *Acyrthosiphon pisum*, and two of its predators. The first predator, the seven-spotted ladybird beetle, *Coccinella septempunctata*, forages primarily on foliage. The second predator, a ground beetle, *Harpalus pennsylvanicus*, forages on the ground as its common name implies. In a factorial design experiment, *C. septempunctata* and *H. pennsylvanicus* ate more aphids when together than the sum of the number each ate separately. The behavioral characteristics that allowed this were the different foraging patterns of the two predators (mitigating IGP) and the defensive response of the shared prey. Typically, pea aphids are found on the plant, and thus are out of the reach of *H. pennsylvanicus*. However, when threatened by a foliage-foraging enemy, pea aphids drop from the plant (Dixon 1958). In Losey and Denno's (1998) experiment, this meant that pea aphids could often escape one type of predator or the other, but had a much more difficult time escaping both at the same time.

In a report published separately, Losey and Denno (1999) elaborated on the temporal aspect of the *C. septempunctata* / *H. pennsylvanicus* / pea aphid system. The seasonal activity patterns of *C. septempunctata* and *H. pennsylvanicus* must overlap in order to produce synergism.

Community-level consequences

Many of the studies reviewed above were primarily aimed at gaining results from a single prey population. However, as seen in the cases involving IGP, the effects of generalist natural enemies may extend beyond the target prey. Studies that use the abundance of various prey and the abundance of different natural enemies as response variables are uncommon but informative. For example, Fagan and Hurd (1994) enhanced the number of mantids in open old-field plots and then calculated the interaction strengths between the mantids and 10 different prey taxa (including intraguild prey). While the mantids mainly had weakly negative interactions with other arthropods, some interactions were strongly negative (such as with nabids), while other were strongly positive (such as with mirids). The positive effects were thought to be due to indirect effects of the mantids killing predators or competitors of the mirids.

Another interesting result from Fagan and Hurd's (1994) study is that not all interaction strengths between mantids and their prey were consistent for the three different initial densities of mantid augmentation. For example, the effect of mantids on aphids changes from strongly negative at low initial mantid augmentation to weakly positive at high initial mantid augmentation. While the underlying mechanism for this change in their interaction is not clear, it may relate to the intraspecific interactions of mantids in the study. Mantid densities converged over the course of the 3-week experiment, as a result of dispersal and mortality, both of which were apparently related to lack of food. The convergence in mantid densities illustrates the idea of "sustainable predator load," and emphasizes the importance of considering the duration of observed effects in the field.

Foraging behavior and other mechanisms of interaction

Although biocontrol is most concerned with population-level patterns, the studies above illustrate how the behavior and other organism-level attributes of particular biocontrol agents influence their ecological interactions. Certain processes can generate antagonism between biocontrol agents. These include interference, such as by IGP, and exploitative competition. Other behaviors, such as avoidance of different natural enemies, behaviors that lead to spatial, temporal, and other types of habitat partitioning, and mutualistic actions, will reduce antagonism. Finally, different biocontrol agents may affect each other indirectly.

As described in some of the cases presented above, the propensity for IGP between natural enemies is an important determinant of what type of joint effects they will have. Additional examples of severe interference come from studies of entomopathogens and insect biocontrol agents. For example, Poprawski et al. (1998) tested the compatibility of two fungi with a ladybird beetle (*Serangium parcesetosum*); all three of these species have been used to manage whiteflies. One of the fungi

(*Paecilomyces fumosoroseus*) did not generate beetle mortality above that observed from the control treatment. However, the other fungus (*Beauveria bassiana*) caused approximately 50% mortality above the control mortality to the beetle when it was ingested. Thus, a combination of *P. fumosoroseus and S. parcesetosum* may be useful for whitefly control, whereas *B. bassiana* and *S. parcesetosum* may be an antagonistic, and possibly disruptive, biocontrol combination.

By the design of the experiment above, the fungi and beetle were assured to contact each other. However, probably due to the physiological interactions of the species involved, only encounters with *B. bassiana* increased the risk of mortality to beetles and generated interference. Analogously, when both natural enemies are freely-foraging individuals, not all encounters will lead to IGP or other substantial interference. McCaffrey and Horsburgh (1982) showed that mutual avoidance between *Orius insidiosus* and *Leptothrips mali* (both species are predators of mites) was the most frequent outcome of their encounters. Therefore, the two species were judged likely to be compatible as biocontrol agents.

However, some of the studies that concentrate on assessing IGP or lack of IGP may not be able to assess exploitative competition (Birch 1957) between biocontrol agents. Obrycki et al. (1998) suggested both IGP and exploitative competition as a possible mechanisms explaining why *Coccinella septempunctata* negatively affects another ladybird beetle, *Coleomegilla maculata*, but not their shared prey. No studies in my survey were designed to measure exploitative competition between biocontrol agents. The mechanisms, however, can be distinguished by extensive observations on relevant aspects of consumer behavior and habitat choice. An experiment that can measure exploitative competition has been performed by C. Rutledge and S. Eigenbrode (pers. comm.). In their experiment, aphids were subjected to two different predators either simultaneously or separately in turns. Decreased predator effectiveness in both treatments indicates exploitative competition .

Partitioning of the environment is a way for species to reduce exploitative and interference competition. Several studies utilize detailed behavioral data on IGP in order to infer some type of habitat partitioning. Some have been described above as explanations for population-level results (as in Chang 1996, Losey and Denno 1998 and 1999). The natural enemies of filth flies (including the house fly, *Musca domestica*) also partition the habitat, in multiple ways. Several species of parasitoids have different humidity preferences (Ferreira de Almeida and Pires do Prado 1999, Geden 1999) and different depths in manure (Ferreira de Almeida and Pires do Prado 1999) in which they prefer to find hosts.

Various sorts of mutualisms have been found between biocontrol agents, and these may increase the joint effect of the mutualists on their shared prey. For example, certain entomopathogenic nematodes harbor symbiotic bacteria. Both the nematode and the bacterial symbiont possess pathogenic properties (Gerritsen et al. 1998). In some cases, neither the nematode nor the bacteria alone is sufficient to kill their host, so the total pathogenicity observed depends on the individual pathogenicities of the nematode and the bacteria, and on the interaction between the two (Gerritsen et al. 1998). Another possible mutualistic relationship may be found between certain predatory insects and entomopathogenic fungi. The seven-spotted ladybird beetle, *Coccinella septempunctata*, consumes aphids that have been killed by a fungus, *Pandora (=Erynia) neoaphidis*, in the field (Chapter 2). In the laboratory, Pell et al. (1997) found that the ladybird beetles do consume fungal spores when eating the *Pandora*-infested cadaverous aphids, thus qualifying the interaction as a case of IGP. However, in the process of consuming cadavers, ladybird beetles will become coated with viable spores and can then effectively vector the fungus to infect healthy aphids (Pell et al. 1997). In terms of laboratory aphid populations, the joint effect of adult *C. septempunctata* and *P. neoaphidis* is additive or synergistic (Roy et al. 1998).

Finally, a study by Evans and England (1996) depicts a subtle yet substantial indirect interaction between two natural enemies that is mediated by the honeydew of aphids. In Utah, the primary pest of alfalfa is the alfalfa weevil, *Hypera postica*. Both the seven-spotted ladybird beetle (*C. septempunctata*) and a parasitoid wasp (*Bathyplectes curculionis*) attack *H. postica*. Complicating the situation, the pea aphid, *A. pisum*, is also found in the system and is attacked by *C. septempunctata*. *B. curculionis* does not attack *A. pisum*, but the honeydew excretion of *A. pisum* does serve as a food source for adult *B. curculionis*. Thus, wasp effects are indirectly enhanced by the presence of a potential pest. Evans and England used a two-way factorial experimental design, with *C. septempunctata* and *A. pisum* being added or not added (Figure 1.6).

In the absence of *C. septempunctata*, addition of *A. pisum* (and its honeydew) augmented *B. curculionis*. However, when both *C. septempunctata* and *A. pisum* were added, *C. septempunctata* preyed upon *A. pisum*, which therefore did not augment *B. curculionis* as greatly. The net result was that the joint effect of augmenting *C. septempunctata* in the presence of pea aphids produced antagonism. Although the antagonism still improved biocontrol, this outcome fuels opinions that the pest management benefits of having *C. septempunctata* in the U.S. may not be worth the toll it takes on North American ladybird beetles (recall Elliot et al. 1996).

Additional considerations: scale

No other study in my survey involves as many species as that by Settle et al. (1996). Their work exemplifies the type of large-scale (both spatially and temporally) experiment that may best influence agricultural practices. In Indonesian rice, a complex of natural enemies checks the populations of several pest species. Pesticide applications lower early-season predator abundance and allow certain pests to suddenly increase while their enemies are recovering. When pesticides are not used, the predator population feeds on detritivores and increases before the pest population increases. This build-up of predators prevents pests from achieving outbreak levels. Other management practices such as asynchronous, small-scale planting, can also boost predator populations. While the role of particular natural enemy species is not clear in this study, together they have a positive effect on pest management.

In addition to the greater extent that larger-scale studies can address the concerns of the farmer, they also highlight another aspect of pest management in practice, that agricultural systems can contain more than one species of pest. This is clear when crop-by-crop compilations of pests are examined (for example Metcalf and Metcalf 1993). We are only starting to develop an understanding of the consequences of multiple biocontrol agents for managing multiple pest species.

Conclusions

While agricultural ecosystems may be depauperate when compared to native habitats (Valladares and Salvo 1999), they will still often contain several interacting species. Multiple potential predator species are often present in biocontrol systems. Predator species may interact with consequences for biocontrol. The best case for biocontrol is synergism, in which the combination of different biocontrol agents improves control beyond what could be attained by adding their individual effects (Losey and Denno 1998). The worst case is disruption, in which the presence of multiple predator species increases pest density above the level obtained with a single biocontrol agent (Rosenheim et al. 1993).

Obviously, both classical and conservation biocontrol efforts should avoid natural enemies that disrupt existing control levels. Furthermore, I suggest that classical biocontrol programs should try to avoid importing species that produce antagonism with native biocontrol agents, particularly if the antagonism is accompanied by a decline in the abundance of the native agents. Antagonism among native species in conservation biocontrol programs is acceptable as long as it does not disrupt pest control. Conservation biocontrol with exotic species that have previously established in a region may pose an ethical quandary. In practice, some habitat modifications for conservation biocontrol may not offer the ability to selectively increase populations of native species without also increasing established exotics.

Mechanistic studies are required to explain and predict which of the several possible pest control outcomes (figure 1.1) will be produced by interactions between biocontrol agents. Gathering mechanistic behavioral data can be extremely time- and labor-intensive (recall Rosenheim et al. 1999). A question that remains unanswered is whether a behavioral approach can be developed to assess the variety of mechanisms by which biocontrol agents interact in systems where experiments are not feasible. In the next chapter, I attempt to quantify behavioral data from a guild of natural enemies of aphids with the objective of inferring their net effect on their shared prey.

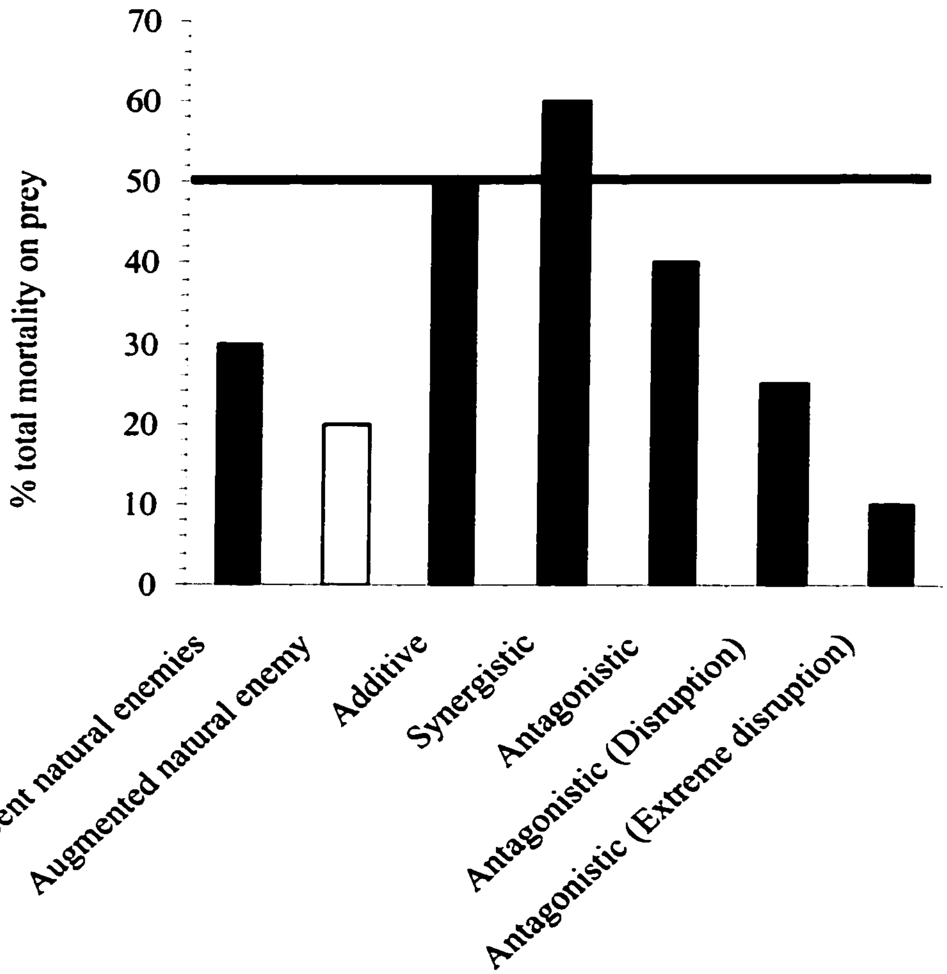


Figure 1.1 Possible outcomes when two natural enemies attack the same prey (modified from Ferguson & Stiling 1996). If incumbent natural enemies (A) inflict 30% and natural enemy B inflicts 20% mortality on their shared prey, then the joint effect of the two predators is *additive* if the mortality that they inflict together equals 50%. When A and B are combined and the total mortality inflicted on the prey is greater than the additive case, then the effect of the two predators is *synergistic*; if the total prey mortality falls below the additive case, then the two predators can be called *antagonistic*. (This set of outcomes is referred to as "non-additive" by Ferguson and Stiling [1996], but I choose to employ the term "antagonistic," which also describes the situation.) Note that antagonistic effects can still improve pest control if the mortality inflicted by both natural enemies is still greater than the mortality inflicted by either of the natural enemies separately. Also, note that studies may measure different response variables, such as pest population size and/or growth rate.

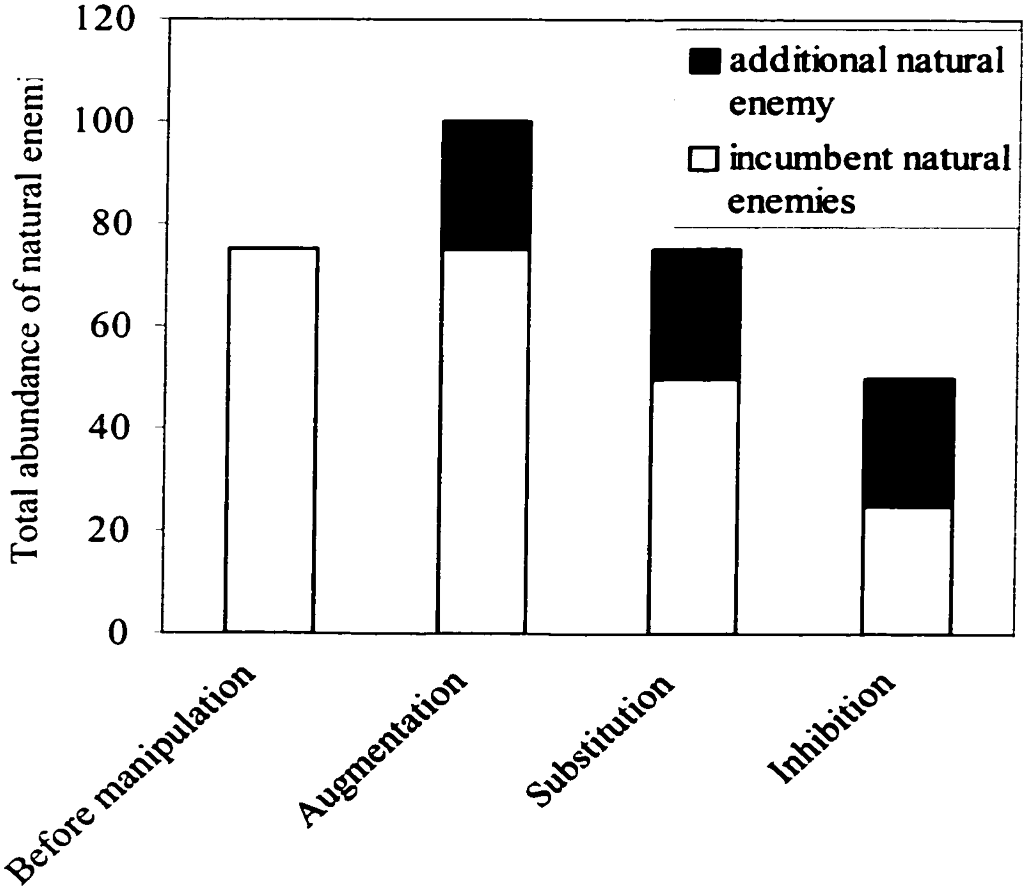


Figure 1.2 Possible outcomes following the addition of a natural enemy to an incumbent guild (*sensu* Root 1967) of natural enemies. If the initial density of natural enemies in an area is 75 individuals and 25 natural enemies are added through either introduction or augmentation, then the new "sustainable load" of natural enemies (Fagan and Hurd 1994, described further below) can increase (*enhancement*), remain the same (*substitution*), or decrease (*inhibition*).

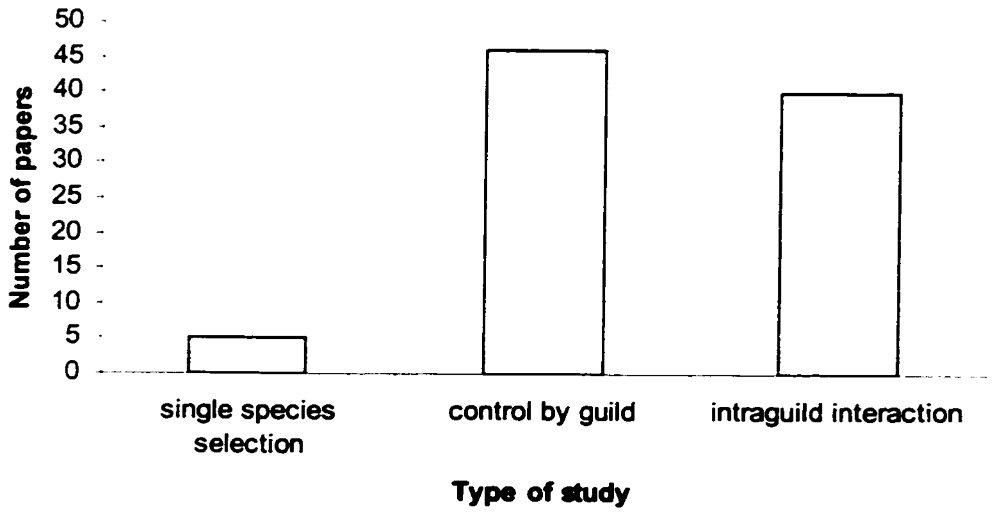


Figure 1.3 Types of studies involving multiple species of natural enemies in Appendix B. For further details on the sample of papers, see text.

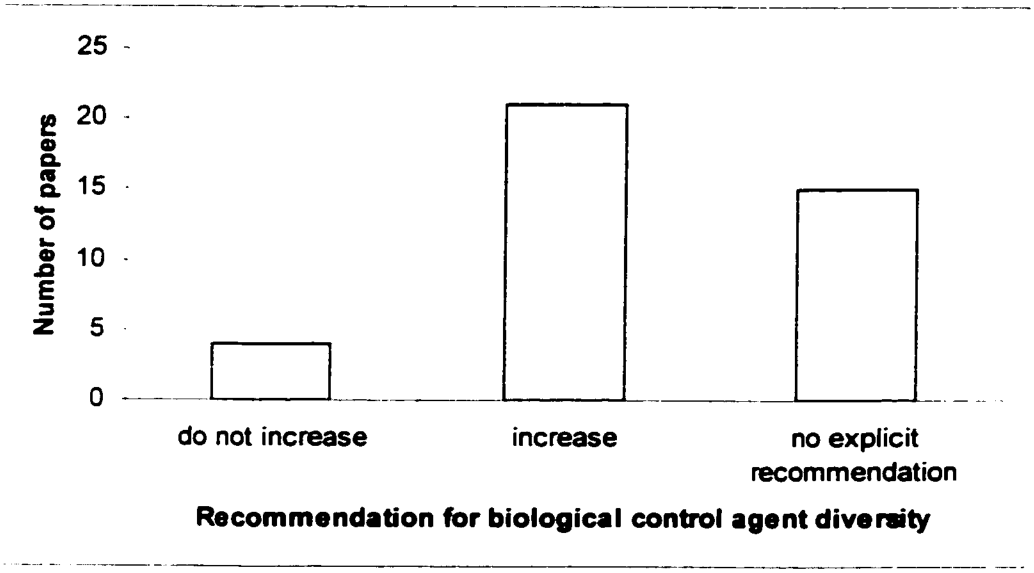


Figure 1.4 Recommendations from recent papers (Appendix B) considering the use of multiple species for biological control.

		Natural enemy A	
		absent	present
Natural enemy B	absent	pest alone	pest + A
	present	pest + B	pest + A + B

Figure 1.5 Two-way factorial experimental design as applied to multispecies biocontrol settings. In this basic design, two natural enemies (A and B) are tested against a pest. The factors manipulated by the experimenter are the presence or absence of each species. This produces the four treatments described inside each box below. The "pest alone" treatment is usually considered the control. The treatment that involves both A and B usually sums the number of individual natural enemies used in the single-species natural enemy treatments, although occasionally those numbers are halved and then summed. This type of experiment tests the degree of pest suppression obtained when biocontrol agents are used singly and in combination and can be readily analyzed using well-developed statistical techniques (i.e. ANOVA; Sokal and Rohlf 1981).

		C. septempunctata	
		not added	added
A. pisum	not added	*H. postica* alone (control)	decreased *H. postica* due to predation
	added	increases *B. curculionis*, which decreased *H. postica*	antagonism due to indirect interaction between *C. septempunctata* and *H. postica*

Figure 1.6 A summary of the study by Evans and England (1996). Each box represents a treatment in their experiment and contains the results obtained for that treatment. The details of their experiment are explained in the text.

Chapter 2

Spatial overlap among intraguild predators and agricultural pests in western Washington pea fields

Introduction

The effects of natural enemies on prey populations range from trivial to devastating (Hawkins et al. 1997). The effectiveness of a predator's foraging behavior can help explain the population-level impact they have on their prey (Holling 1959). Spatial complexity can reduce the ability of predators to forage effectively and create relative prey refuges (Huffaker 1958). Even the morphology of an individual plant is sufficiently complex to generate relative refuges for insects from their predators (Kareiva and Sahakian 1990). On some plants predators have difficulty walking on leaf surfaces (Marks 1977), which limits their access to prey on those surfaces (Grevstad and Klepetka 1992).

Since plant architecture can modify predator-prey relationships, it may alter interactions among natural enemies. Different predators show different preferences in where they forage on plants (Chang 1996). In agroecosystems, several species of natural enemies often occur (Chapter 1). These species may interfere with each other as they forage, reducing their effectiveness as biological control agents (Force 1974, Ehler and Hall 1982, Briggs 1993). Different natural enemies may even attack one another, an interaction called intraguild predation (IGP; Polis et al. 1989, Polis and Holt 1992) Intraguild predation can disrupt biological control (Rosenheim et al. 1993, Rosenheim et al. 1995, Rosenheim 1998). On the other hand, multiple natural enemies may provide better pest control if they attack pests in different locations (Chang 1996, Losey and Denno 1998, Losey and Denno 1999).

The extent that different predators overlap in space may be an important factor determining whether multiple natural enemies help or hinder biological control efforts. Relatively few studies contain quantitative data on freely-foraging arthropods in open field settings. In one example, the foraging behaviors of ladybird beetles and ground beetles are so different that they present an inevitable tradeoff in risk for their prey (Losey and Denno 1998). This produces synergism between these predators and impacts prey populations more than the sum of the individual impacts of the two predators.

As another example, Rosenheim et al. (1999) describe a large dataset of observations on a green lacewing, *Chrysoperla carnea*, foraging on cotton. In 448.6 cumulative hours of observations, lacewing larvae were attacked 9 times by intraguild predators (5 hemipteran species). Lacewings were also occasionally IGP predators (Rosenheim pers. comm.). The observations of lacewings as IG victims supported results from a field cage study that found that the combination of predatory hemipterans and lacewings decreased the level of aphid control achieved by lacewings alone (Rosenheim et al. 1993). Disruption of biocontrol was due to the overlap in the foraging patterns of lacewings and hemipterans on cotton. Overlap in foraging causes lacewings and hemipterans to encounter each other. During these encounters, hemipterans can attack and kill lacewings, and thereby disrupt the effect of lacewings.

Rosenheim et al.'s 1999 data required a remarkable amount of time to assemble, approximately 50 hours of observation per event in which lacewings were IGP victims. The striking message is that IGP events occur rarely on a behavioral timescale, but frequently enough to affect the shared prey's population. Therefore, to quantify encounter rate and behavior-on-contact requires massive amounts of observation. Yet such data, as well as incidental natural history obtained through observation, establish both the context and mechanisms that influence populations and communities. The basic challenge to be met is that encounters between predator and prey tend to be infrequent.

I have made similar observations on predator foraging in western Washington peas (*Pisum sativum* L.) fields. Elsewhere I have reported some results from 782 minutes, or 13 hours, of observing laboratory-reared larvae of a green lacewing, *Chrysoperla plorabunda* (Chang 1998). Although pea aphids (*Acyrthosiphon pisum*) were numerically the most abundant potential prey, thrips (mostly *Frankliniella occidentalis*) where the prey most consumed by larval *C. plorabunda*. Out of 34 encounters between larval *C. plorabunda* and other insects, only three were with other natural enemies: two encounters with mummies (dead aphids containing developing parasitoids) and one encounter with a minute pirate bug (*Orius* sp.). Only one of these three encounters led to IGP; a *C. plorabunda* larva consumed a mummy. These results suggest that *C. plorabunda* may control thrips more effectively than pea aphids. However, the sample size was too small to allow drawing inferences about interactions between *C. plorabunda* and other biocontrol agents in the field.

The overlap in foraging behavior among and within species may complement encounter data. Because prey items are not evenly distributed on different host plant parts, the overlap between potential predators and prey should be assessed to suggest which potential prey are more likely to be encountered. Similarly, because IGP also depends on predators actually encountering each other, overlap between different predators should be assessed. This suggests two interesting questions:

1) How often does IGP occur relative to predation on herbivores?
2) How much do predators overlap with each other and with herbivores?

Materials and methods

Description of study sites and general natural history

Observations were made at three sites: the Rent's Due Ranch (RDR: 48°14′N, 122°22′W), an organic farm located just outside Stanwood, Washington, and two research farms (Sumner: 47°11′N, 122°13′W; and Fife: 47°12′N, 122°20′W) in the Washington State University extension station system. RDR was a study site only in 1997, while Sumner and Fife were studied from 1997 to 1999. These sites differ from each other in certain details of management practices and the composition of the ecological community.

The focal crop for this study was peas (*P. sativum*, var. Maestro). Peas are grown on approximately 43,500 acres in Washington (National Agricultural Statistics Service 1997). At RDR, peas are planted in the spring, whereas I planted peas in Sumner and Fife in the late spring or summer, depending on the planting condition in each year (Table 2.1). In addition to peas, the vegetation at the sites included numerous weeds. I controlled weeds manually by hoeing when necessary through the summer.

The natural history of the animals present at these sites is briefly summarized in Appendix C. The guild (Root 1967) of species consuming peas was identified during the course of behavioral observations, population surveys, collection of voucher specimens, and casual observation. They include several aphid species (e.g. *A. pisum, Aphis fabae, Myzus persicae*), thrips (*F. occidentalis*), whiteflies (*Trialeurodes vaporariorum*), the spotted cucumber beetle (*Diabrotica undecimpunctata*), plant bugs (*Lygus* sp.), the pea leaf weevil (*Sitona lineatus*), and unidentified mites (Acari), leafhoppers (Cicadellidae), caterpillars (Lepidoptera), and slugs (Stylommatophora).

The arthropod herbivores are prey to several different natural enemies. I have collected at least six species of web-building spiders (*Tetragnatha laboriosa, Araneus diadematus, Lepthyphantes tenuis, Theridion bimaculatum, Zygiella* sp. and *Erigone* sp. or spp.) and observed jumping spiders (Salticidae) and wolf spiders (Lycosidae) infrequently. Harvestmen (*Phalangium opilio*) are detritivores but will eat live aphids in the lab (pers. obs.). Centipedes (Chilopoda) are another non-insect predator present at my sites, but do not seem to climb vegetation.

The majority of the predatory species are insects that belong to six orders: Hemiptera, Thysanoptera, Neuroptera, Coleoptera, Diptera, and Hymenoptera. The Hemiptera are represented by three species, all of which are omnivores: *Nabis alternatus, Geocoris* sp. and *Orius tristicolor*. Adults of an unidentified predatory banded-wing thrips (Thysanoptera: Aeolothripidae) are readily distinguishable from the herbivorous thrips on peas by its black and white coloration.

Both green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobiidae) occur at my sites. At least two species of green lacewings have been found; one, *Chrysoperla plorabunda*, is predacious in the larval stage but not as an adult, while the other, *Chrysopa* sp. (possibly *C. oculata*) is predacious in both the larval and adult stage.

Predatory Diptera at my sites include several unidentified species of Syrphidae (including a *Syrphus* sp.) and a predacious gall midge, probably *Aphidoletes aphidomyza*. These predacious Diptera are predators as larvae but not as adults.

Ladybird beetles (Coleoptera: Coccinellidae) are predacious as larvae and as adults, and are represented by 8 species: *Coccinella septempunctata, Coccinella undecimpunctata, Harmonia axyridis, Hippodamia convergens, Adalia bipunctata, Cycloneda pollita*, and 2 unidentified species. At least three species of ground beetles (Coleoptera: Carabidae) have been collected: *Pterostichus melanarius*, *Amara* sp. and *Bembidion* sp. Unidentified rove beetles (Staphylinidae) and soldier beetles (Coleoptera: Cantharidae) infrequently forage on peas.

Hymenoptera include parasitoids, predators, and omnivores. Three species of primary parasitoids (species that attack herbivores) have been observed: *Aphidius ervi*, a second *Aphidius* sp., and *Praon* sp. At least one unidentified species of hyperparasitoid (a parasitoid that attacks primary parasitoids) has been collected as well. At least three species of aphid-hunting wasps (Sphecidae) prey upon aphids located on peas: *Pemphredon* sp., *Psenulus* sp., and *Diodontus* sp. Finally, two species of ant (Formicidae) occasionally venture into peas: *Mymica* sp. and *Lasius* sp. These ants do not tend aphids at the study sites.

Finally, I found two fungal pathogens infecting aphids (*Pandora neoaphidis* and *Entomophthora chromaphidis*). Detritivores in the system include earwigs (*Forficula auricularia*), which may attack small, defenseless prey. Springtails (Collembola) and earthworms (Oligochaeta) also occur and may provide alternative prey for some of the predators.

Certain “transient” species were seen rarely in peas (i.e. as few as once in three years) and are unlikely to have impacted my behavioral observations. However, these transients (which include a frog, killdeer, crows, sparrows, cats, dogs, rabbits and deer) may have affected population-level patterns in the system (Chapter 3).

Species abundance

To characterize the density of herbivorous insects and inactive predators, I sampled the organisms on pea plants over the course of each summer. These data will be presented in more detail in the following chapter. For now, these data are pooled for each year. The number of plants examined was 608 in 1997 (Chang 1998), 885 in 1998, and 1,296 in 1999.

Herbivore locations and pea aphid surveillance

To determine where aphids and other relatively sedentary insects are located on individual plants, I inspected pea plants and recorded the location of every insect observed. For this survey, a total of 64 plants were examined at various times during 1998 and 1999. Plant parts were categorized as leaf edge, leaf surface, tendril, axil, stem, bud, flower, or pod.

I attempted to estimate the encounter rate between aphids and predators during the 1999 field season using a video camera recorder (Sony DCR-TR7000) to monitor individual pea aphids for extended periods of time. Focal aphids were chosen haphazardly. I positioned the video camera to film focal aphids for sessions generally lasting approximately one hour at a time at various times during the day. Tapes were later viewed, and behavioral and demographic events were noted.

Focal predator observations

To measure where natural enemies forage on individual plants, my field assistants and I observed haphazardly chosen, freely foraging individual predators. Observers attempted to follow continuously an individual for at least 15 minutes, or until the focal insect was lost. Observation periods were occasionally extended beyond 15 minutes if an encounter or series of encounters took place that required additional time to determine the outcome of the event. Observations were also discontinued if focal insects obviously reacted to the observer; this was sometimes the case for big-eyed bugs, which will stand still on the soil in response to observers.

In addition to encounters and their outcomes, I also recorded the activities of the focal predators. The categories of activities included resting, grooming, foraging, feeding, being fed upon, and mating. I also noted whether predators were located on or off of pea plants, and the part of the plant upon which the predator was situated (if applicable). The parts of the pea plant were the same as for the herbivores. During the latter portion of the 1999 field season, I distinguished between upper and lower leaf surfaces.

A total of 4,752 minutes (79 hours) was spent observing predators from 1997-1999; at least 26 different taxa were watched (Table 2.2). Observations were spread out temporally over the growing season (Table 2.3) as well as on a daily basis.

Index of probability of encounter

The degree to which different species overlap in microhabitat use may be an important factor in encounter rates. In order to highlight the overlap in foraging behavior of several of these predators, as well as their overlap with the distribution of their prey, I employed a simple index. Numerous indices have been utilized to quantify similarity in traits between two groups (for examples, see Martinez Pico 1965, Horn 1966, Schoener 1970). I have decided to use an index that reflects the chance that two individuals will be found on the same microhabitat at the same time. This index of overlap for two species (A and B) is based on the assumptions of no interactions between the individuals and a random distribution of foraging over time, and can be represented as equation 2.1:

$$\sum_i a_i \times b_i \qquad \text{for } i = 1 \ldots n \text{ different microhabitats} \qquad \text{Equation 2.1}$$

$a_1, \ldots a_n$ = the proportion of time spent in each microhabitat by species A

$b_1, \ldots b_n$ = the proportion of time spent in each microhabitat by species B

While this index could be modified to incorporate more realism (such as by scaling a_i and b_i by the relative area of each microhabitat), the limitations of my data do not warrant such action. One feature of this index is that values can be compared to weigh the probabilities of intraspecific to interspecific encounters.

Statistics

I used a G test to test whether the observed distribution of encounters differed from the expectation that prey would be eaten in the same proportions as their abundance. A *G* test was also used to test whether the kill rates of various predators differed from each other. To analyze whether herbivores and natural enemies differed in their ability to escape being eaten after an encounter with a potential predator, I performed a 2 × 2 test of independence using a *G* statistic with Williams' correction (Sokal and Rohlf 1981).

Results

Species abundance

For survey data pooled from all sites across all summers, individual herbivores outnumbered individual predators by a ratio of greater than 9:1 (Figure 2.1). The most abundant species was the pea aphid, which accounted for 69% of all individuals. From sampling individual peas, the most abundant predators were parasitoids (in the form of mummified aphids), a pathogenic fungus (cadavers of aphids killed by this fungus were particularly abundant in 1999), and syrphid flies of various stages of development (Figure 2.2).

Prey distribution and behavior

Pea aphids and other potential prey showed different distributions on individual pea plants. The positions of 1,060 individual arthropods were recorded on various dates in 1998 and 1999. For most species with multiple individuals in this sample, the greatest percentage of individuals was located on leaf surfaces (Figure 2.3). In 1999, 85% of the pea aphids found on leaf surfaces were on the lower leaf surface. Upper and lower leaf surfaces were not distinguished in 1998.

Video camera surveillance of pea aphids revealed little information, except that encounters between aphids and natural enemies seem rare. No predation events occurred during 9.5 cumulative hours of recording a total of 228 pea aphids (over 180 aphid-hours). Only two demographic events were filmed, both of which were births of pea aphid nymphs.

Temporal patterns

Patterns in arthropod abundance and predator behavior can be distinguished for at least three temporal scales: year-to-year, within-season, and circadian patterns. Insects differed in their abundance in each of the three years of this study. Differences can be found in the relative contributions to the guild of predators by individual species over this time (Figure 2.2).These may have been produced by variation in the weather during each of these summers, particularly during the early part of the summer when peas grow the most. Of the three years during which this study was conducted, 1997 seemed most typical for western Washington. Temperatures were close to average in June and July, although precipitation was above average. However, relatively less rain fell during the period in which peas were growing in Sumner. In 1998, the entire summer was hotter and drier than average. In 1999, the summer was wetter and cooler than typical in the early part of the growing season (Table 2.4).

Within-season differences occur in the arrival of active stages of each natural enemy species in the field. Although my observations were not designed to detect differences in when species appeared, the dates on which each species was first observed during a summer provide a rough approximation of species arrival (Figure 2.4).

Finally, while precise data are lacking, clearly predators varied in the time of day during which they prefer to forage (Figure 2.5). Hunting wasps (*Pemphredon* sp., *Psenulus* sp., and *Diodontus* sp. were indistinguishable in the field) were noticeably active only a few hours, typically during the hottest part of the day around the early afternoon. Coccinellids tended to be most active during daylight hours, although some were observed foraging at night. Parasitoids became active at about dawn, reduced activity during midday, then resumed foraging in the evening until dusk. Syrphid larvae tended to be most active in the early morning (until dew evaporated), stopped foraging during midday, then resumed foraging in the evening and possibly overnight. Nabids appeared to forage steadily 24 hours a day, but moved more quickly during daytime. Harvestmen and carabids were active mostly, but not exclusively, at night. Daily patterns were not obvious in the foraging behavior of other predators.

Focal predator encounters

Encounters between individual predators and prey were generally infrequent. Several observations were made of insects apparently reacting to the presence of another insect without physical contact occurring, but these can be ambiguous events and so I did not include them in further analyses. If only cases of physical contact are considered, 156 encounters were observed between arthropods from 1997-1999 (Figure 2.6). This translated into an average encounter rate of less than two per hour per individual predator. Analysis of the guild of foraging arthropod predators reveals that the observed encounter rate with different prey types was roughly proportional to the abundance of the various prey types in the field ($G = 1.69$, df = 3, $0.5 < P < 0.9$, $n = 156$).

The encounter rates and capture percentages by particular predators within the natural enemy guild differ (examples in Figure 2.7). Some of the predators in the guild, such as ladybird beetles and lacewings, are relatively generalized and attempt to feed on whatever they encounter and are able to subdue. On the other hand, parasitoids and hunting wasps had more restricted diets. Hunting wasps had a significantly higher rate of pea aphid kills than parasitoids, chrysopids, syrphids, and coccinellids (Figure 2.7, $G = 11.43$, df = 4, $0.01 < P < 0.025$, $n = 53$). The rates of pea aphid capture for parasitoids, chrysopids, syrphids, and coccinellids were statistically indistinguishable ($G = 0.27$, df = 3, $0.9 < P < 0.975$, $n = 47$).

Six cases of strict intraguild predation were observed (Figure 2.7, Table 2.5). The proportion of IGP to other trophic interactions was not significantly different from the proportion of IG prey individuals to individual herbivores ($G = 3.12$, df = 1, $0.05 < P < 0.1$, $n = 156$).

Foraging behavior of predators

In addition to the differences in the daily foraging patterns between predator species, predators also differed in their location on pea plants (Figure 2.8). Syrphid larvae are the only predators that spent the greatest portion of their time foraging on leaf surfaces. Coccinellids, lacewing larvae, and damsel bugs all spent the greatest portion of their time on leaf edges. However, the second greatest amount of time is spent on stems by coccinellids, leaf surfaces by lacewings, and on the ground by damsel bugs. Parasitoids and minute pirate bugs preferred pods, and big-eyed bugs spent the majority of their time on the ground.

These results do not account for the development of pea plants, and thus may be biased against flowers and pods, which are present for only a portion of the growing season. Flowers in particular are present for a relatively short period of time.

Behavioral overlap

While the overlap between different predators with each other was generally low, the overlap between predators and pea aphids was even lower (Table 2.6). The average probability of finding two predators on the same microhabitat was 0.19, while the probability of finding a predator on the same microhabitat as a pea aphid was 0.08.

Discussion

The relatively low overlap between predators and pea aphids is primarily due to the fairly high fraction of pea aphids (40%, Figure 2.3) located on leaf surfaces. Most predators do not spend much time foraging on leaf surfaces. The greatest percentage of time spent by a predator on leaf surfaces is 29% (by syrphid larvae, Figure 2.8). Waxes on pea plant surfaces make them difficult to grip for many foraging predators (Eigenbrode et al. 1998). Therefore, while waxes help pea plants maintain water balance, they also provide a relative refuge for pea aphids. Pea aphids may achieve pest status through the combination of the relative refuge and their intrinsically high reproductive capacity.

Pea aphids also appear to have better defensive abilities than thrips, the second most abundant herbivore at the sites. Both pea aphids and thrips attempted to evade attackers by walking, running, or flying, but the percentage of encounters that resulted in successful captures of thrips was higher (Figure 2.6). Pea aphids can also kick away smaller attackers (Evans 1976) such as parasitoids and early instar predators. However, evasion tends to be a better defense than kicking. In 19 encounters with lacewing larvae, seven pea aphids escaped capture by dropping from the plant, six walked away, and six were eaten (Chang 1998). Although dropping from the plant is an effective way to escape an oncoming natural enemy, it is also a risky behavior (Dill et al. 1990). In full sun, the soil can be very inhospitable for pea aphids, as the surface can reach lethal temperatures and overheating leads to paralysis and death. When the soil surface temperature is 42° C, first instar pea aphids are paralyzed in as little as 2.8 minutes, while adults are paralyzed in 6.2 minutes (Roitberg and Myers 1979). Furthermore, pea aphids become much more vulnerable to ground foraging predators (Losey and Denno 1998).

Although the spatial overlap of predators is generally greater with other natural enemies than with the most abundant herbivores (Table 2.6), the frequency of intraguild predation appears to occur in proportion to the availability of intraguild prey in this system. This may be because the mobile natural enemies have better sensory abilities than herbivores that make them more likely to recognize natural enemies without contact. Furthermore, while not statistically significant, IG encounters are less likely to result in a successful capture than encounters between predators and thrips or pea aphids (Figure 2.6). The taxa that were IG victims were the most abundant of the guild of natural enemies in peas.

The key question from a biocontrol standpoint is whether IGP occurs to a degree that disrupts pest control in this system. Here "disruption" means that the pest population becomes higher than it would be if only the single best natural enemy attacks the pest (Chapter 1). Extrapolating a pattern at the level of behavioral events to population-level patterns is not straight-forward. Some mathematical theory provides guidance in connecting predator behavior, IGP, and prey suppression (reviewed by Rosenheim et al. 1995). Theoretical analyses of IGP have often emphasized equilibrium conditions (Hassell 1978, Polis et al 1989, Polis and Holt 1992, Schreiber and Gutierrez 1998) and must be applied cautiously to the annual, highly-disturbed pea field system where this study took place. The models also contain fewer species (Figure 2.9) than I observed interacting. However, comparing the general models to the data from this study suggests that IGP should not disrupt biocontrol in this system.

The analytical models of Hassell (1978), Polis et al. (1989), Polis and Holt (1992), and Schreiber and Gutierrez (1998) differ in their evaluation of the significance of IGP for prey suppression, but agree that it is important to compare IG predators and IG victims in their ability to exploit prey. The superior exploiter is the predator that would suppress the prey to a lower level when it is the only natural enemy in the system. The models agree that to improve pest control, the better exploiter must be in the system. When the IG predator is the better exploiter, IGP does not disrupt pest control when the system reaches equilibrium. Instead, pest suppression is always at least the level that the IG predator provides alone, although the IG predator may exclude the

IG victim from the system. When the IG victim is the superior exploiter, IGP can disrupt biocontrol.

IGP is less detrimental to pest control in Hassell's (1978) model based on interactions among two parasitoids and one prey (Figure 2.9a). IG victims that are superior exploiters can coexist with IG predators. As long as neither destabilizes the system by searching randomly, prey populations are lower in three-species systems. A tritrophic model (Schreiber and Gutierrez 1998) of two natural enemies, a herbivore, and a host plant (Figure 2.9d) produces similar results. Models based on classical competition models (Polis et al. 1989, Polis and Holt 1992; see Figure 2.9b and c) find IGP to be more disruptive. In these models, if the IG predator is the inferior exploiter it always depresses IG victim populations and always disrupts prey suppression.

If the comparative data on rate of pea aphid capture is an acceptable approximation of exploitative abilities, then IGP observed among some of the predators in the system should not disrupt pea aphid control. Only hunting wasps had a distinguishably high rate of pea aphid capture. Hunting wasps did not suffer from IGP during the observation period. It does not seem likely that hunting wasps would suffer IGP from the other arthropod predators in this system, for several reasons. First, hunting wasps are much more mobile than the rest of the natural enemy guild and would appear to be able to easily evade their attacks. Second, the foraging method of hunting wasps is primarily aerial, in contrast to the foraging of the other natural enemies. Hunting wasps land on plants only rarely while searching, and often appear to grab aphids without touching the plant. The combination of speed and aerial foraging is so distinct that I was unable to develop a method to compare hunting wasp foraging preferences with those of the other predators. Finally, hunting wasps were only common in 1998, which may indicate some segregation from the other predators at a large temporal scale. It is possible that web-building spiders, another group with a distinct (and, for this study, incomparable) foraging behavior might capture hunting wasps, but this too seems unlikely. In this study, the most abundant spiders were dwarf species (*Erigone* sp. or spp.). These spiders are small and found mostly at the base of pea plants, where hunting wasps do not venture.

The pea aphid kill rates of several other natural enemies in the system were statistically indistinguishable. Of these, coccinellids and chrysopid larvae were intraguild predators, while parasitoids (as larvae within dead aphids) and syrphid larvae were intraguild victims (Table 2.5). Only two IGP incidents seem to be cause for concern: the big-eyed bug that consumed a syrphid larva, and the ant that also consumed a syrphid larva. Big-eyed bugs consumed pea aphids in laboratory arenas (pers. obs.; ants were not tested). Due to limited observations on big-eyed bugs and ants, I only observed them attacking syrphids in the field. Big-eyed bugs and ants are both generalist predators and have potentially positive roles in biocontrol (Readio and Sweet 1982, Perfecto and Castinieras 1998). On the other hand, examples exist of big-eyed bugs and ants disrupting biocontrol as well. Big-eyed bugs are among the hemipterans that disrupt lacewing biocontrol in cotton (Rosenheim et al. 1993, Rosenheim et al. 1999). Ant-homopteran mutualisms are well known (Holldobler and Wilson 1990), and can disrupt biological control (Perfecto and Castinieras 1998). However, ants did not appear to tend aphids in this study. The IGP encounter between the ant and syrphid larva occurred on the soil and was not the result of the ant defending any aphids.

The temporal occurrence of IGP must also be considered when connecting behavioral and population-level phenomena. The IGP by the big-eyed bug and the ant both occurred at the end of the growing season, in late August 1998 (Figure 2.10). By that time, pea aphid populations had crashed and it is possible that the predators still in the field faced a shortage of herbivorous prey. Furthermore, although pea plants were still at the Sumner site, most peas were harvested before that time. Because this is an annual system, late-season IGP events are unlikely to damage biocontrol by syrphids. Further work should be done to assess whether such rare events are ecologically important.

Behavioral results are most useful to the practice of biocontrol when they are linked to population-level patterns. The foraging patterns and encounters of the natural enemies in western Washington peas suggest that they do not disrupt each other. In the next chapter, I present empirical data from augmentation experiments of IG predators that suggests that they did not disrupt biocontrol by resident natural enemies in this system.

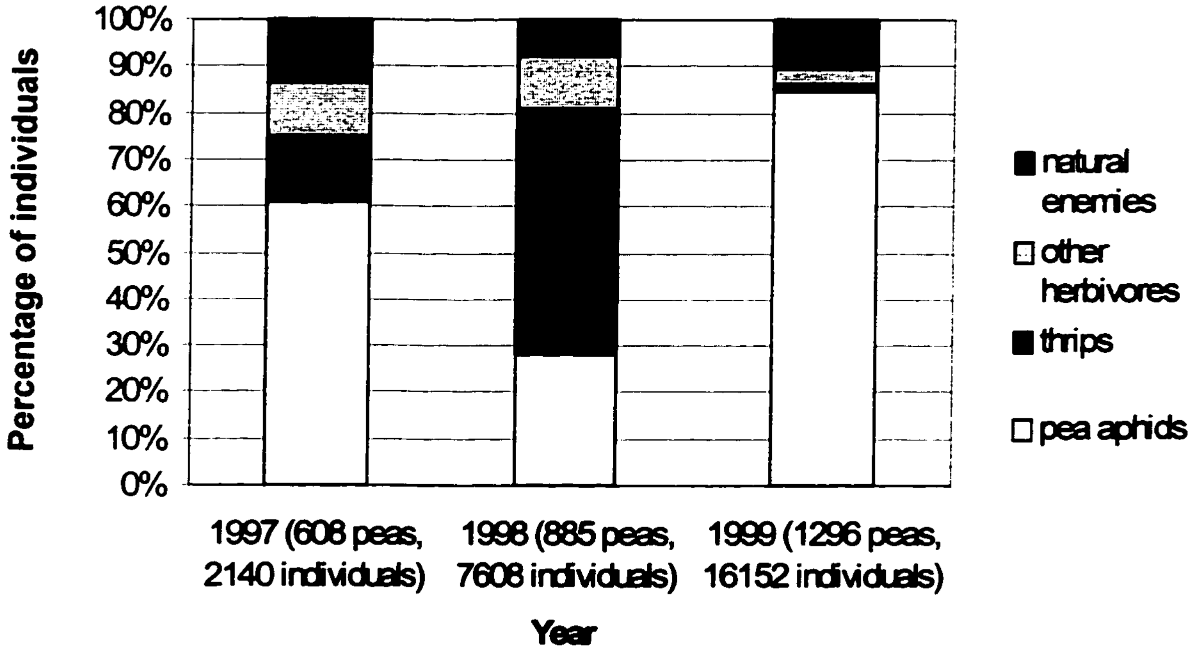


Figure 2.1 Organisms associated with peas in 1997, 1998, and 1999. These data were collected by visually examining individual pea plants. Following each year in parentheses are the total number of pea plants in Sumner and Fife inspected for population sampling and the total number of individual organisms found on those plants. The y-value for each of the four groupings (pea aphids, thrips, other herbivores, and natural enemies) is the fraction of the total number of individuals belonging to each grouping.

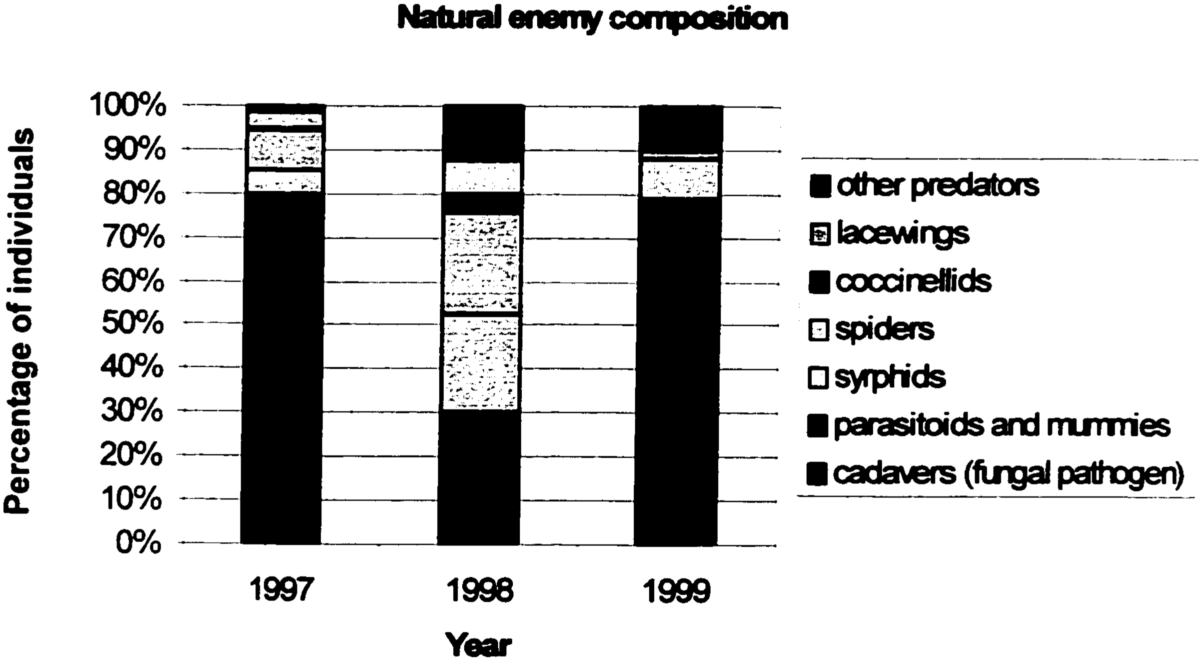


Figure 2.2 Natural enemies found on peas, 1997 - 1999. These are the data grouped under "natural enemies" in Figure 2.1. The y-value for each natural enemy grouping is the percentage contributed by each taxon to the total number of individual natural enemies. For each taxon, all individuals of any life stage were considered. Cadavers are dead aphids that had been infected by fungi, primarily "Other natural enemies" includes hemipterans, banded-wing thrips, *Aphidoletes aphidomyza*, and ants.

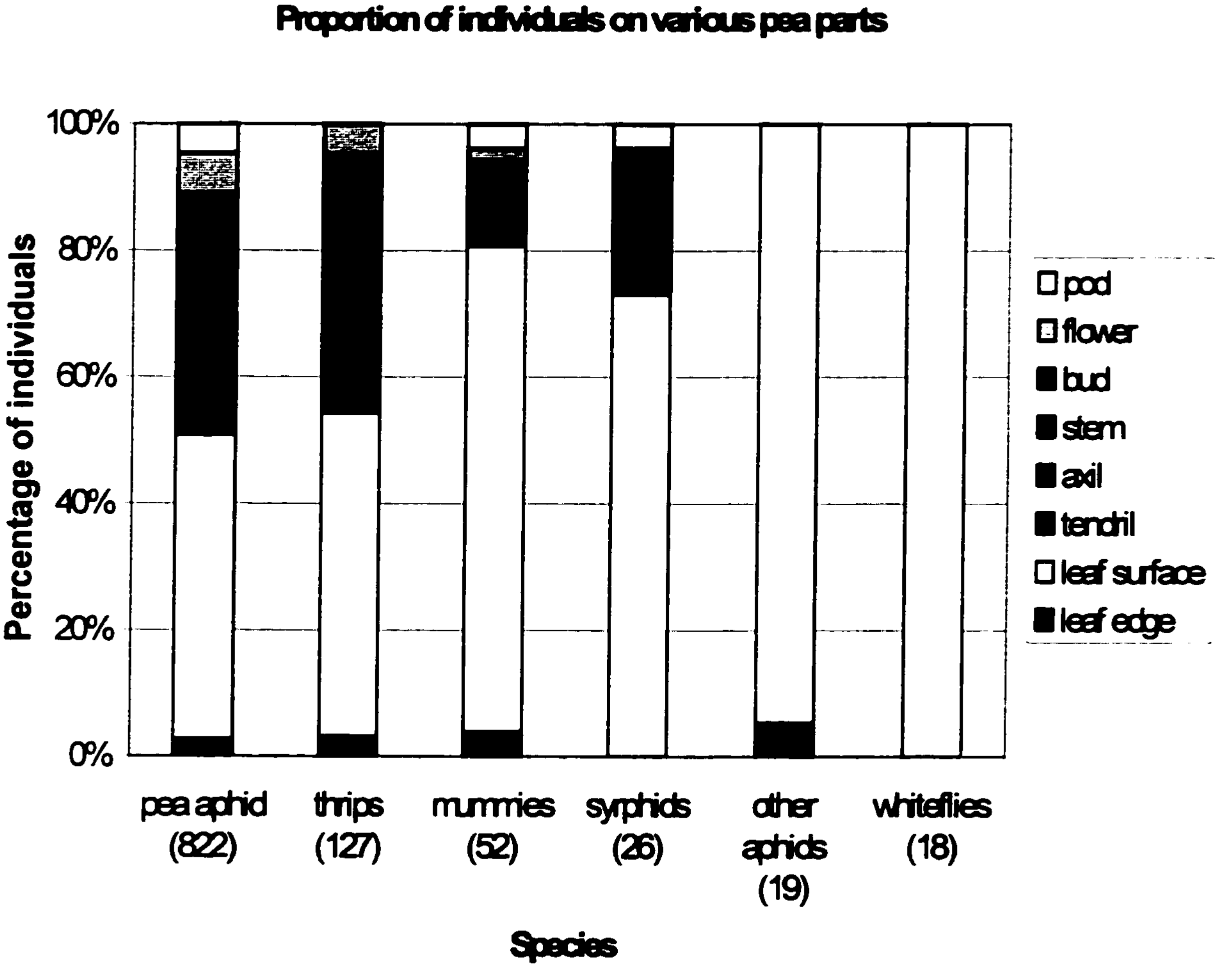


Figure 2.3 Locations of every individual insect on 64 pea plants sampled at various times during 1998 and 1999. Locations were classified as: leaf edge, leaf surface, tendril, axil, stem, bud, flower, or pod. The number in parentheses after each species name represents the number of individuals of that species in the sample of 64 plants.

Week of	**First sighting of:**
23-Apr-99	Seven-spotted lady bird beetle
30-Apr-99	
7-May-99	Parasitoid
14-May-99	
21-May-99	Eleven-spotted ladybird beetle, harvestman, big-eyed bug
28-May-99	Damsel bug, syrphid fly, fungal pathogen
4-Jun-99	
11-Jun-99	Green lacewing
18-Jun-99	
25-Jun-99	
2-Jul-99	Hunting wasp
9-Jul-99	Minute pirate bug
16-Jul-99	

Figure 2.4 Timeline of first records of natural enemy species during 1999. Each date reflects the first observation of a particular species during the summer, whether made during population sampling, behavioral observations, or casual observation.

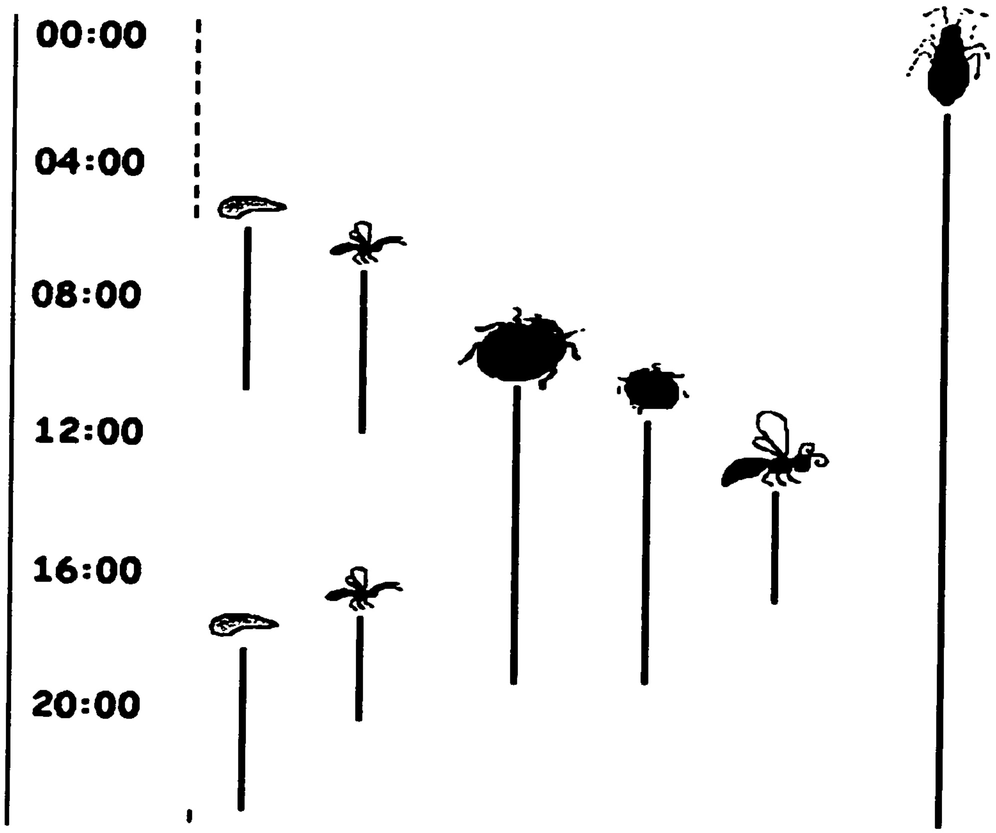


Figure 2.5 Daily activity patterns for selected active-foraging predators. Icons from left to right represent: 1) syrphid larvae, 2) parasitoid wasps, 3) seven-spotted ladybird beetle, 4) eleven-spotted ladybird beetle, 5) hunting wasps, and 6) damsel bugs. Solid lines indicate the times during which various insects are most active. Dashed line indicates period in which few observations were made. Primarily nocturnal arthropods such as carabids and harvestmen are not pictured.

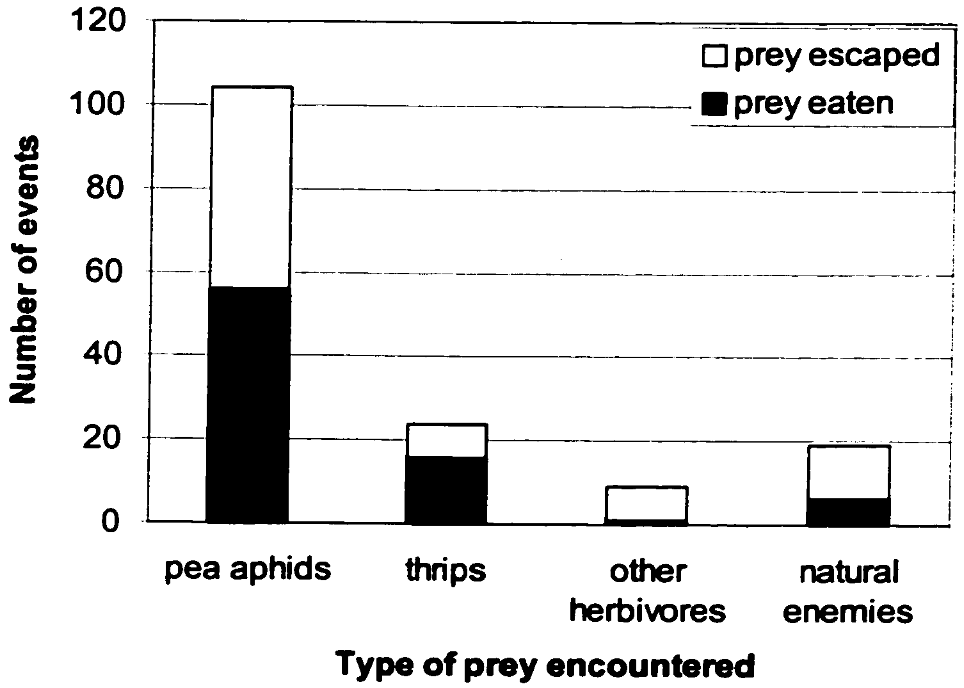
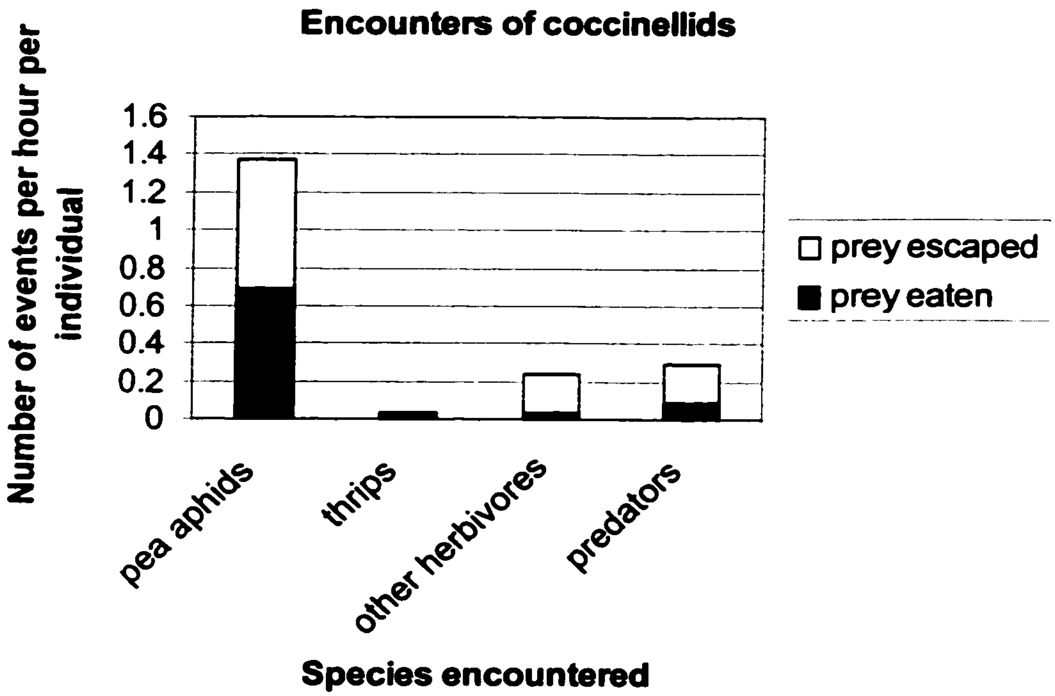
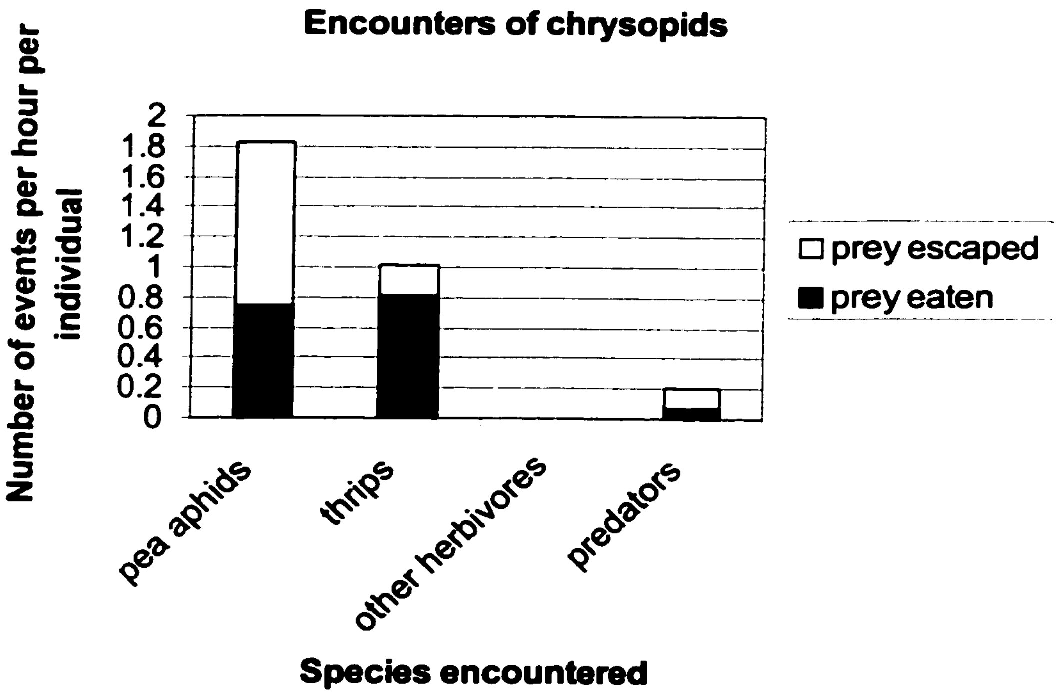


Figure 2.6 Outcomes of encounters between predators and potential prey in peas. Predators, parasitoids, and pathogens are included in the group of "natural enemies." Composition of taxa is given in Appendix 2.1.

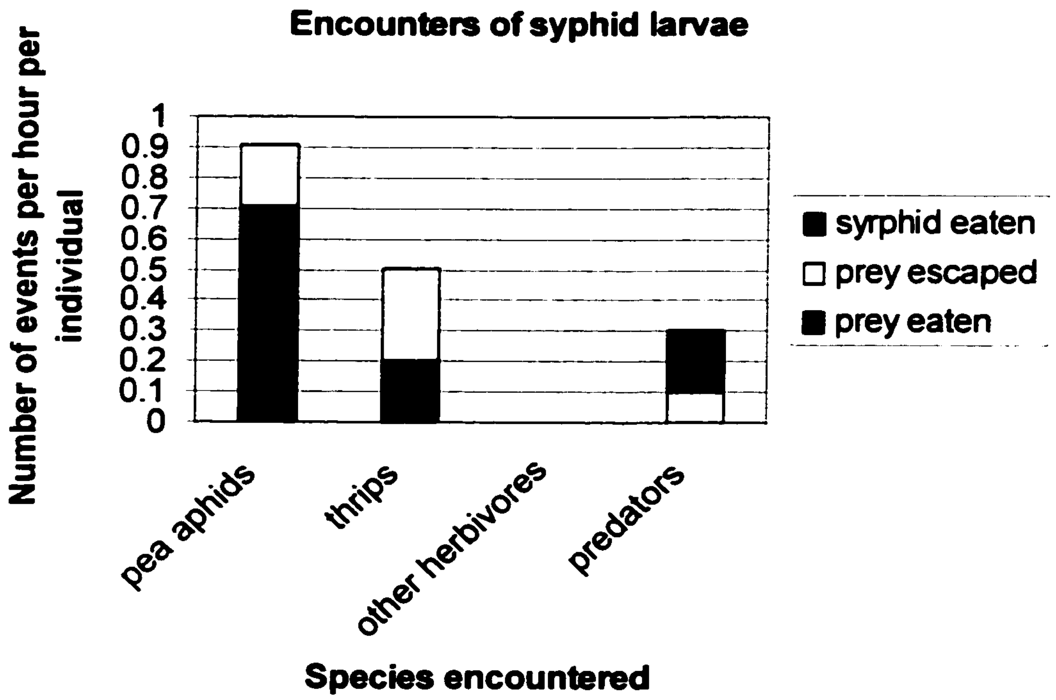
a.


Encounters of coccinellids
Number of events per hour per individual
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
pea aphids
thrips
other herbivores
predators
Species encountered
□ prey escaped
■ prey eaten

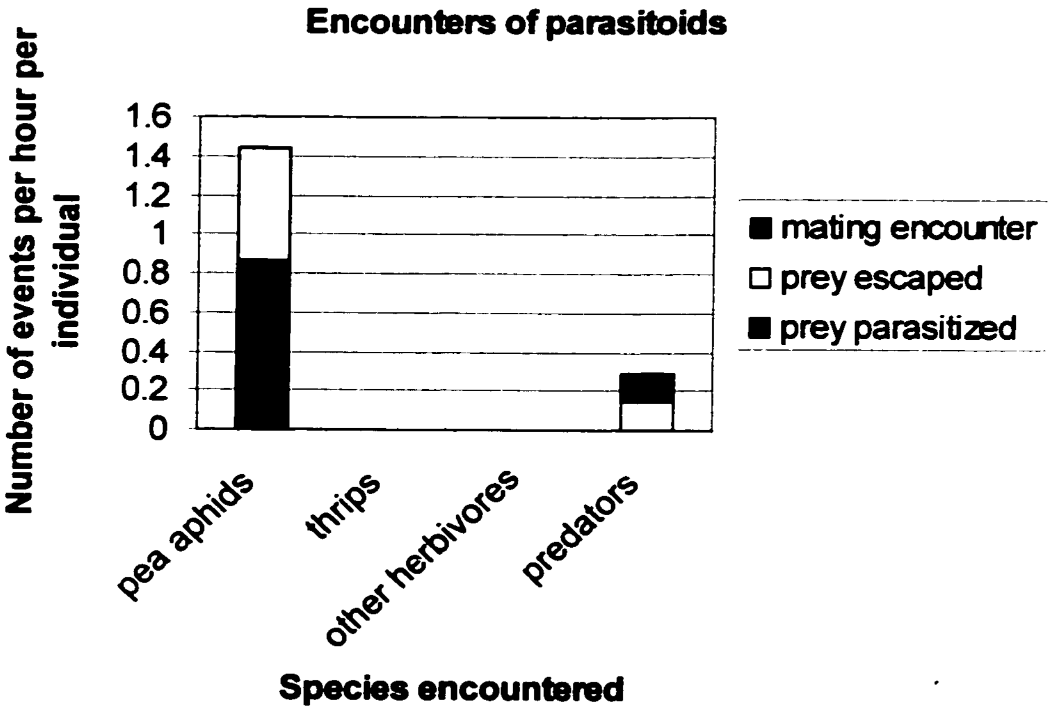
b.


Encounters of chrysopids
Number of events per hour per individual
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
pea aphids
thrips
other herbivores
predators
Species encountered
□ prey escaped
■ prey eaten

c.


Encounters of syphid larvae
Number of events per hour per individual
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
■ syrphid eaten
□ prey escaped
■ prey eaten
pea aphids
thrips
other herbivores
predators
Species encountered

d.


Encounters of parasitoids
Number of events per hour per individual
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
■ mating encounter
□ prey escaped
■ prey parasitized
pea aphids
thrips
other herbivores
predators
Species encountered

e.

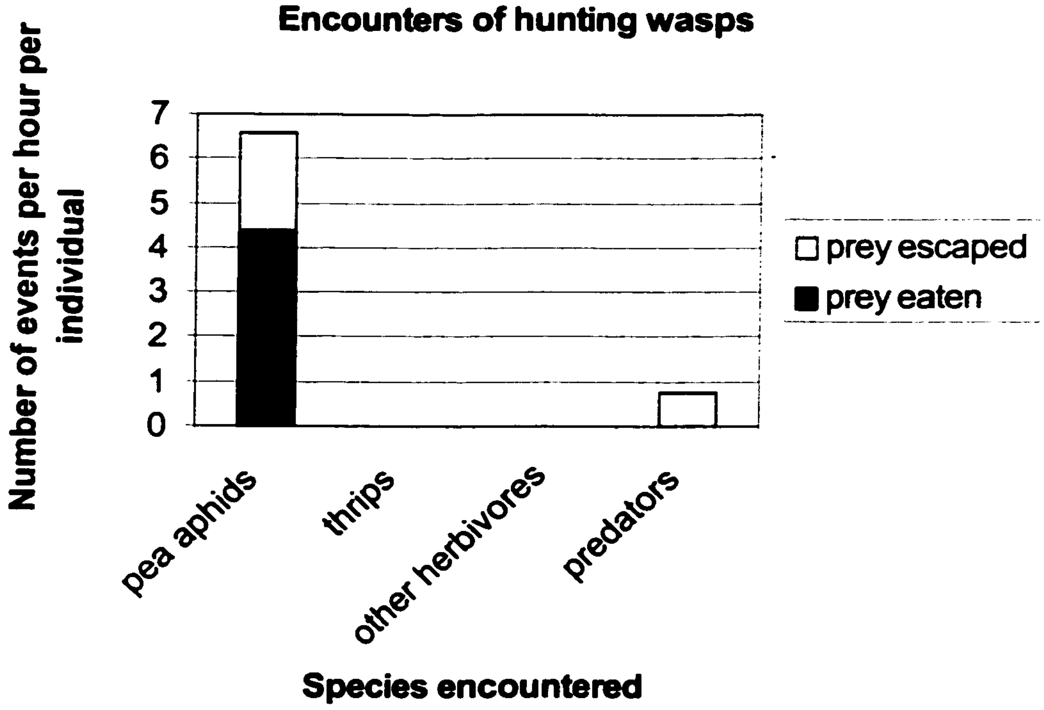


Figure 2.7 Outcomes of encounters between predators and potential prey, by taxa. Figure 2.7 a. Coccinellids are composed of larval ladybird beetles (which are difficult to identify to species in the field) and adult *Coccinella septempunctata*, *C. undecimpunctata*, *Harmonia axyridis*, *Hippodamia convergens*, *Cycloneda pollita*. Figure 2.7 b. Outcomes of encounters between chrysopids and potential prey. Chrysopids include larval *Chrysoperla plorabunda* (including data from Chang 1998) and both larval and adult *Chrysopa* sp. Figure 2.7 c. Observations on larval syrphids. Adult syrphids are herbivores, so on their foraging behavior is not included in this figure. Figure 2.7 d. Encounters between parasitoids and other insects. *Aphidius ervi* is the most common parasitoid at the study sites. The category of "predators" includes conspecifics. Figure 2.7 e. Encounters between hunting wasps and other insects. Hunting wasps include *Pemphredon* sp., *Psenulus* sp., and *Diodontus* sp. These are difficult to resolve to species in the field. Note that the encounter rate (y-axis) is over three times higher for hunting wasps than for the predators with the next highest encounter rate, chrysopids (Figure 2.7 b).

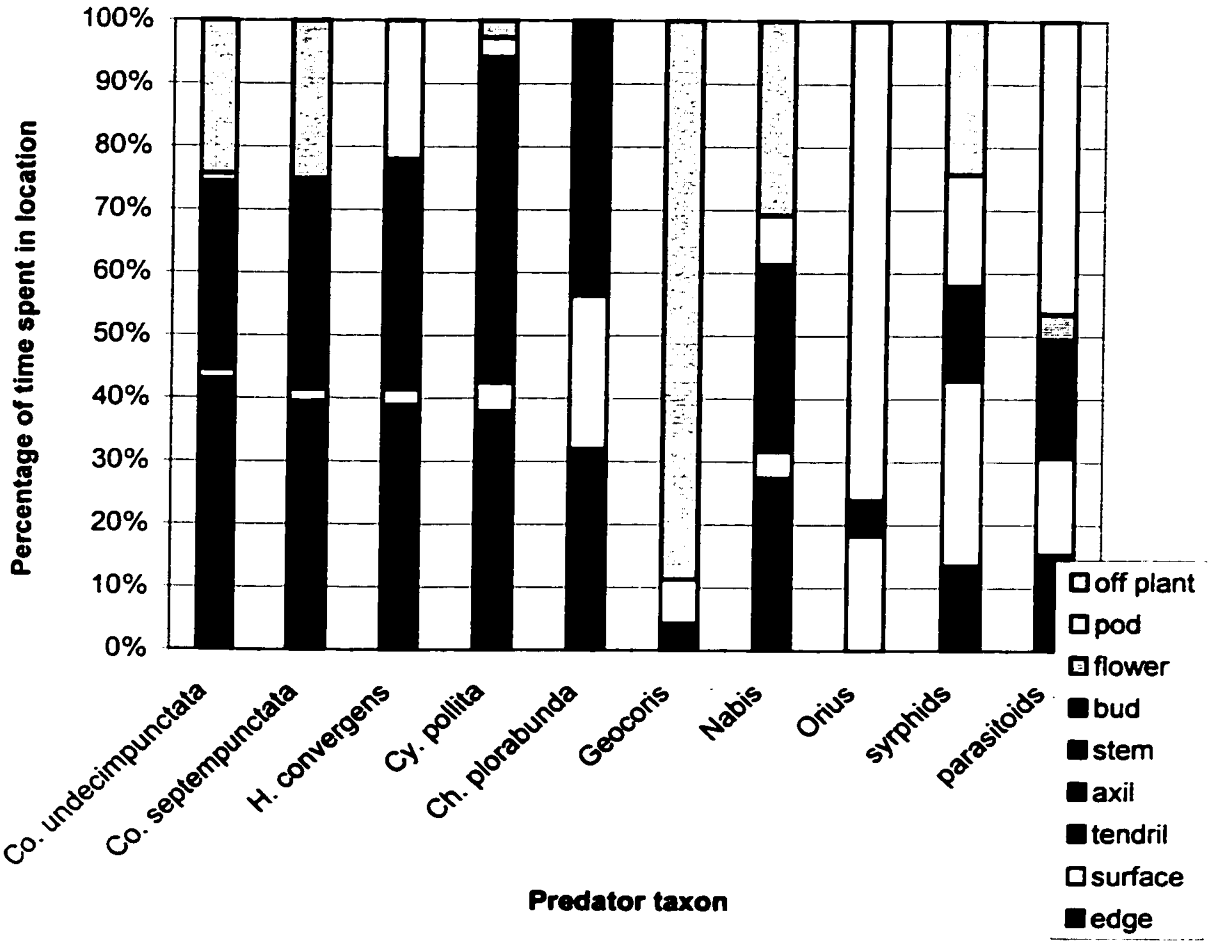
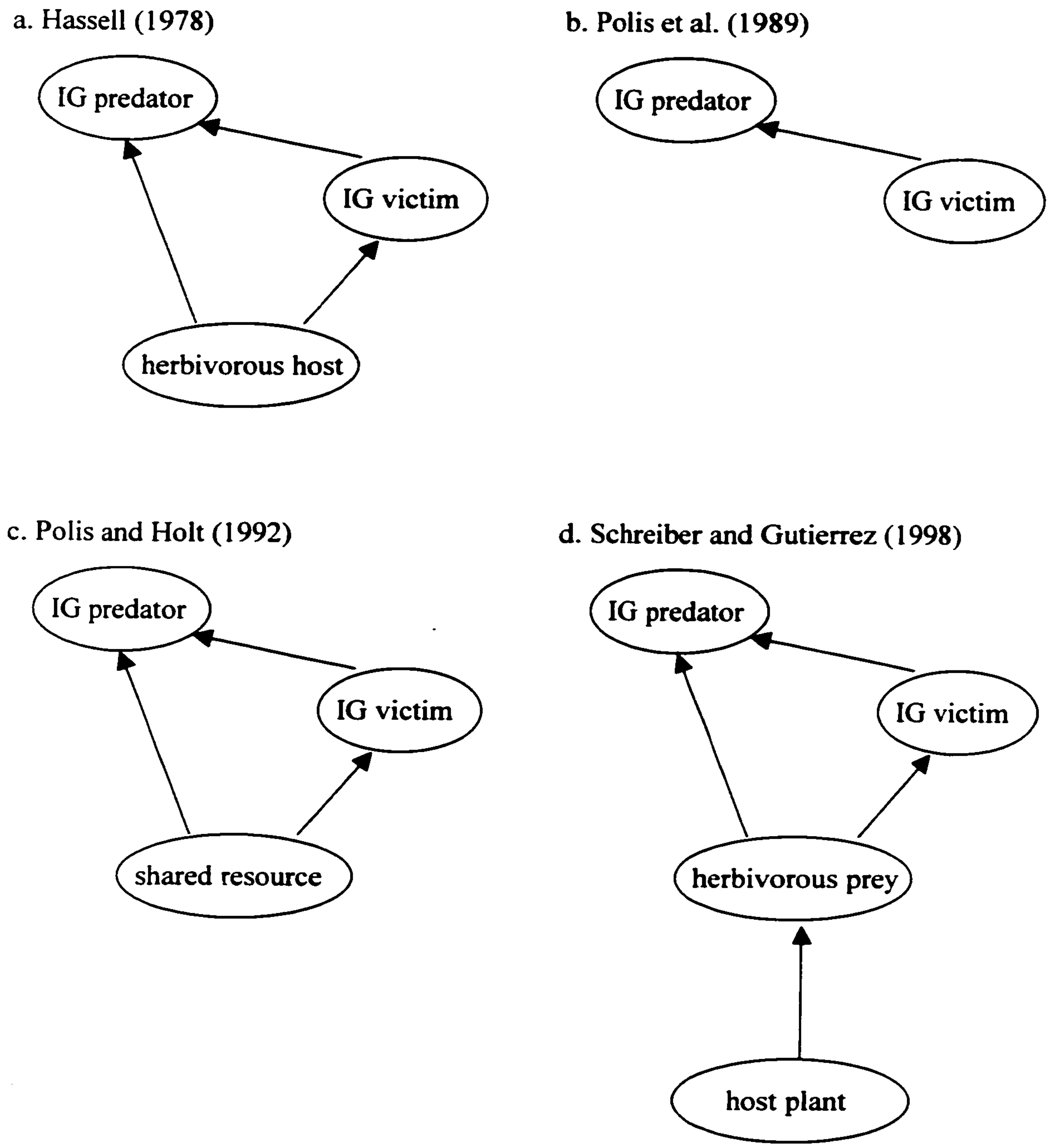


Figure 2.8 Predators differ in where they allocate their foraging time on peas. Classification of pea parts is explained in the "Methods" section of this chapter. Common names of predators can be found in Appendix 2.1. Only larval syrphids are considered in this figure. Hunting wasps do not appear in this figure because the majority of their foraging time is spent in the air. Hunting wasps occasionally land on plants or the soil when attacking or handling aphids, but do not seem constrained by plant architecture.



a. Hassell (1978)

b. Polis et al. (1989)

c. Polis and Holt (1992)

d. Schreiber and Gutierrez (1998)

Figure 2.9 Summary of mathematical models of IGP in biocontrol.

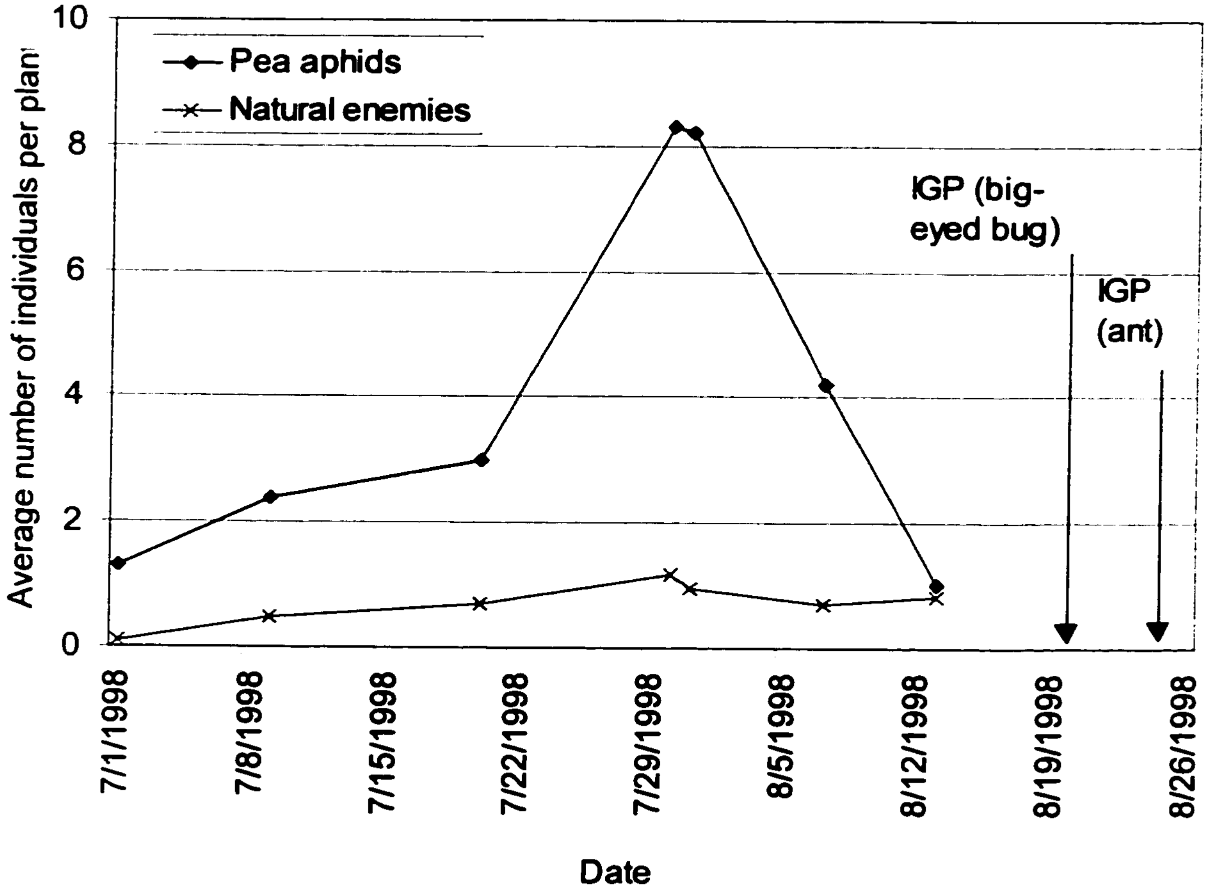


Figure 2.10 Seasonal occurrence of IGP events involving a big-eyed bug and an ant . In both cases, the IG victim was a syrphid larva. Both events were observed after pea aphid densities had crashed at the Sumner site. Because peas are an annual crop, IGP that occurs after aphids crash may not affect pea aphid dynamics.

Table 2.1 Planting dates and plot design at research farm sites.

Year	Site	Planting date	Number of plots	Plot size
1997	Fife	July 7 & 9	9	0.5 × 32 m
	Sumner	June 19, 21, 23, 25	19	3 × 3 m
1998	Fife	April 9, 16, 23, 28	10	2 × 8 m
	Sumner	June 16 & 17	6	2 × 8 m
1999	Fife	May 2 – 5	12	2 × 2 m
	Sumner	May 11	6	2 × 5 m

Table 2.2 Cumulative minutes spent observing focal predators, by taxonomic group. Certain taxa are difficult to distinguish in the field, and therefore are lumped into one group. Other taxa have distinct larval and adult forms that are considered separately.

Taxa watched (scientific names not listed here can be found in Appendix 2.1)	Number of individuals	Cumulative minutes
adult seven-spotted ladybird beetle	37	1094
Chrysoperla plorabunda larva	36	825*
ladybird beetle larvae (all Coccinellidae)	25	606
syrphid larvae (all Syrphidae)	28	596
parasitoids (*Aphidius* spp.)	50	416
damsel bug	24	327
adult eleven-spotted ladybird beetle	20	258
harvestman	20	153
banded-wing thrips	5	101
hunting wasps	71	82
adult green lacewing (*Chrysopa* sp.)	2	56
hyperparasitoid	5	33
minute pirate bug	5	30
big-eyed bug	8	28
adult ladybird beetle (*Cycloneda pollita*)	1	24
unidentified adult ground beetles	5	24
adult multicolored Asian ladybird beetle	1	18
rove beetles	2	17
adult convergent ladybird beetle	1	17
adult ground beetle (*Pterostichus melanarius*)	2	14
syrphid adults (all Syrphidae)	9	10
wolf spider	3	7
lacewing (*Chrysopa* sp.) larva	1	7
dwarf spider	2	7
ant *(Myrmica)*	1	1
unidentified adult ladybird beetle	1	1

*Includes minutes of observation reported in Chang (1998).

Table 2.3 Seasonal distribution of focal predator observations.

Year	Date of first observation	Date of last observation
1997	June 26	September 9
1998	July 10	September 17
1999	June 14	September 3

Table 2.4 Weather during the growing season, 1997 – 1999. Monthly average temperature and precipitation data from Sea-Tac International Airport weather station, obtained from the Western Regional Climate Center (2000).

Year	**Monthly average**	**June**	**July**	**August**
1997	Temperature (°C)	15.23	18.02	19.85
	Precipitation (cm)	4.16	3.05	3.22
1998	Temperature (°C)	15.48	19.77	19.31
	Precipitation (cm)	2.82	1.04	0.89
1999	Temperature (°C)	14.52	16.90	18.20
	Precipitation (cm)	4.72	3.00	2.34
51 year average	Temperature (°C)	15.72	18.22	18.20
	Precipitation (cm)	3.66	2.01	2.79

Table 2.5 Incidents of intraguild predation and other unusual trophic interactions, 1997-1999.

Intraguild predator	**Intraguild prey**
Lacewing larva (*C. plorabunda*) (see Chang 1998)	mummy (*Aphidius* sp.)*
Ladybird beetle larva	mummy (*Aphidius* sp.)
Big-eyed bug (*Geocoris* sp.)	syrphid maggot
Ant (*Myrmica* sp.)	syrphid maggot
Adult seven-spotted ladybird beetle (*C. septempunctata*)	syrphid maggot
Adult seven-spotted ladybird beetle (*C. septempunctata*)	cadaver (fungal pathogen)‡
Spotted cucumber beetle**	cadaver (fungal pathogen)

*A mummy is a dead aphid containing a developing parasitoid; *Aphidius ervi* is the most common pea aphid parasitoid at the study sites.

‡A cadaver is an aphid that has been killed by a fungal pathogen. The most common fungal pathogen at the sites is *Pandora neoaphidis*. Cadavers retain fungal spores after the death of the host.

**Spotted cucumber beetles are typically herbivorous; therefore, this incident may not qualify as strict IGP.

Table 2.6 Probability of two individuals foraging in the same microhabitat, calculated using Equation 2.1. The number in each cell represents the probability that an individual of the species in the column will be located on the same part of a pea plant as an individual of the species in the row. This does not necessarily mean that the individuals will be foraging on the same plant, just the same part of a plant. Plant parts are defined as in the text. Thus, two individual eleven-spotted ladybird beetles will be found on the same part of the plant(s) that they are foraging on 28% of the time.

	C-11	C-7	*Geocoris*	*Nabis*	*Orius*	parasitoids	syrphid larvae
C-11	0.28	0.28	0.24	0.23	0.02	0.09	0.14
C-7	0.28	0.28	0.24	0.22	0.01	0.09	0.15
Geocoris	0.24	0.24	0.79	0.29	0.01	0.02	0.24
Nabis	0.23	0.22	0.29	0.24	0.07	0.10	0.15
Orius	0.02	0.01	0.01	0.07	0.62	0.38	0.19
parasitoid	0.09	0.09	0.02	0.10	0.38	0.28	0.16
syrphids	0.14	0.15	0.24	0.15	0.19	0.16	0.21
pea aphids	0.05	0.06	0.03	0.04	0.11	0.12	0.15
thrips	0.05	0.05	0.04	0.08	0.29	0.21	0.21

Chapter 3

Augmentation of incumbent generalist predators does not disrupt biological control by resident natural enemies in pea fields.

"The struggle between man and insects began long before the dawn of civilization, has continued without cessation to the present time, and will continue, no doubt, as long as the human race endures." – S. A. Forbes (quoted in McKelvey 1972).

Introduction

The perfect pest control method would prevent or eliminate pest outbreaks without harming anything else. Of course, it is difficult to find practical ways to kill pests without harming non-target species. One possible solution to this problem is to augment non-pest species to biologically control pests. This may be achieved by releasing laboratory-reared individuals or by modifying the habitat to protect and increase resident populations of biocontrol agents. Traditionally, the first method is called augmentative biocontrol, while the second is called conservation biocontrol, although the two methods can be considered end points of a continuum (Ehler 1998).

Case studies demonstrate the feasibility of both augmentative and conservation biocontrol (Debach 1974, Ehler 1998). For instance, augmentative releases of green lacewings have succeeded in improving pest control in various greenhouse crops (Scopes 1969, Hassan et al. 1985, Tauber et al. 2000). Settle et al. (1996) provided an excellent example of how modifying land use practices can increase the abundance of resident predators and reduce insect pests at a large scale in Indonesian rice. While such case studies are promising, several challenges must be met before augmentative and conservation biological control can be used as widely as pesticides or even the classical biological control method of importing exotic natural enemies (Ehler 1998, Tauber et al. 2000).

The impediments to successful augmentation in any particular system range from biological to distribution and marketing (Tauber et al. 2000). One of the biological issues is the degree to which different species of biocontrol agents are compatible. In systems where multiple species of natural enemies attack the same prey, the net effect of the enemy guild on the prey population varies (Myers et al. 1989, Ferguson and Stiling 1996, Chapter 1). In some cases, different natural enemy species produce greater prey suppression (for example Losey and Denno 1998), while in others, natural enemies interfere with each other, which reduces their impact on the target prey (Rosenheim et al. 1993, Rosenheim et al. 1995). Some understanding of the mechanisms of species interactions helps explain these contrasting results. Biological control can be improved when biocontrol agents differ in where they forage, when they forage, the life stages they attack, or the prey densities they attack (Debach 1974, Murdoch et al. 1984, Takagi and Hirose 1994, Chang 1996, Losey and Denno 1998). On the other hand, the efficacy of biocontrol may be limited when agents interfere with each other (Force 1974, Ehler and Hall 1982, Briggs 1993). However, it is possible for the net effect of multiple biocontrol species to increase despite interference among them (Snyder and Wise 1999).

Intraguild predation (IGP) can be considered a particularly strong form of interference (Polis et al. 1989). IGP among biocontrol agents can disrupt pest control and increase pest densities (Polis et al. 1989, Polis and Holt 1992, Rosenheim et al.

1993, Rosenheim et al. 1995, Fagan et al. 1998). Observations of IGP are widespread in biocontrol systems, but reports of it increasing pest populations are still rare (Rosenheim et al. 1995, Hodge 1999). Rosenheim et al.'s (1995) literature review found 45 published reports of IGP among predatory biocontrol agents. Twenty-six of these did not examine the consequences for the populations of shared prey (the target pest). The studies that did examine prey populations found every possible outcome (Figure 3.1). Therefore, interference may occur at the behavioral level, but not result in population-level disruption (see also Snyder and Wise 1999). General mathematical models of IGP indicate that the equilibrium population density of the prey will not be lowered by IGP among natural enemies unless the IGP victim is a superior exploiter of the shared prey relative to the IG predator (Hassell 1978, Polis et al. 1989, Polis and Holt 1992, Schrieber and Gutierrez 1998).

Therefore, to predict the potential for disruption by an IG predator, one must know some biological details about the potentially interacting species. Some natural history and behavioral information from a field pea (*Pisum sativum* var. Maestro) system are presented in Chapter 2 and summarized below in the methods section. This chapter builds on the behavioral study of arthropods in pea fields. Three specific questions are addressed with population and community-level data.

First, *what impact do resident natural enemies have on pea aphid populations?* In western Washington, a variety of natural enemies inflict mortality on pea aphids (*Acyrthosiphon pisum*) (Chapter 2). The level of biocontrol provided by these resident natural enemies should be assessed before discussing whether an IG predator can disrupt biocontrol. Ideally, an experimental enemy removal method would be used to establish the preexisting level of biocontrol. This could be accomplished by applying a insecticide that kills natural enemies but not aphids (an "insecticide check;" Debach 1946, Debach and Bartlett 1951) Due to the time and personnel constraints on this study, such experiments were not performed. Instead, it is inferred that resident natural enemies may limit, but not reduce, pea aphid densities on the basis of population-level observations supplemented by the behavioral observations of the previous chapter.

Second, *does augmentation of a confirmed IG predator disrupt biocontrol by resident natural enemies?* Several controlled experiments were performed in which a confirmed IG predator was augmented for biological control at rates that are realistic for commercial growers. The encounter rates of the augmented predators with pea aphids was essentially equal to the encounter rates of IG prey with pea aphids (Chapter 2). Under these conditions, IGP theory (Hassell 1978, Polis et al 1989, Polis and Holt 1992, Schreiber and Gutierrez 1998) suggests that augmentation will not disrupt biocontrol. That is, the predator augmentation is predicted to decrease densities of pea aphids. The density of intraguild prey is predicted to decrease as well. Data were collected to test these predictions.

Finally, *what is the potential for interference, particularly IGP, among resident natural enemies?* In other words, does IGP among resident natural enemies seem likely to disrupt attempts at conservation biocontrol in pea fields? I examined spatial correlations among the species in the system to make inferences about the potential for IGP among the resident natural enemies in the system. A positive correlation between two natural enemy species may indicate that they are more likely to encounter and interfere with each other, while a negative correlation may indicate that interference is less likely. However, two natural enemies may be positively correlated with each other because they are both tracking densities of their shared prey. Therefore I performed a multivariable analysis of the community.

Methods

Natural history of the system

The experiments were performed on two Washington State University research farms located in Fife (47°12'N, 122°20'W) and Sumner (47°11'N, 122°13'W), Washington. Washington state accounted for over 45% of the 83,691 hectares of regular green peas grown in the U.S. in 1999 (USA Dry Pea & Lentil Council 1999). The pea aphid is the primary pest of field peas in western Washington. Pea aphids damage host plants directly by removing sap and indirectly by acting as a vector of plant viruses (Dunn and Wright 1955, Yencho et al. 1986, Metcalf and Metcalf 1993). Insecticides are often required to reduce pea aphid populations below economically damaging levels (Yencho et al. 1986). In 1996, 79% of the acreage of peas in Washington state was treated with a total of 22,700 pounds of insecticide, mostly methyl parathion (National Agricultural Statistics Service 1997). A recent agreement between pesticide companies and the Environmental Protection Agency has cancelled the use of methyl parathion on succulent peas and several other crops (Rossi 1999).

Natural enemies may help control pea aphid populations. At least 40 species of potential natural enemies of the pea aphid have been identified in Fife and Sumner (Chapter 2). This guild (Root 1967) can be further subdivided into fungal pathogens (2 species), parasitoid wasps (2 species), and arthropod predators (potentially 36 species, 8 of which have been directly observed feeding on pea aphids in the field). The fungi and parasitoids are relatively specialized on pea aphids, while in contrast many of the predators will attack other herbivores found on peas, such as thrips. Some of the predators have been observed killing intraguild prey, such as mummified aphids (which contain developing parasitoids), cadaverous aphids (which are hosts for fungus), and relatively vulnerable predators such as syrphid larvae.

Theory indicates disruption from IGP if the IG victim is the superior exploiter or if IGP occurs disproportionately to predation on herbivores (Hassell 1978, Polis et al. 1989, Polis and Holt 1992, Schreiber and Gutierrez 1998). Neither condition has been found in this system (Chapter 2). IG predator taxa such as lacewing larvae and ladybird beetles do not differ significantly from IG prey taxa in aphid kill rates. IGP events occur in proportion to IG victim abundance.

General organization and sampling method

This study involved three easily recognized spatial scales: individual plants, plots of pea plants within a farm, and the two farm sites. The study was designed to treat farms as blocking factors. However, during the course of the study, major differences in the insect communities between Sumner and Fife became apparent. The differences in insects between the two sites may have been caused by landscape differences (see below). I consider experiments at the sites two separate experiments, rather than blocks of the same experiment. Annual differences in the insect communities were also striking, so experiments in different years are considered separate. Therefore, this study contains five experiments: Sumner 1997, Fife 1998, Sumner 1998, Fife 1999, and Sumner 1999.

In the experiments, treatments were applied at the plot level. Sampling of plots consisted of surveys of randomly-selected individual plants. To survey a plant I visually inspected its height, number of leaves, flowers, and pods. Then I counted every arthropod on the plant. Most of the arthropods involved are essentially stationary and are most accurately sampled visually (versus sweep netting or other capture techniques). Mobile arthropods could potentially have been counted multiple times on different plants, although this is unlikely due to the generally low density of mobile species. On the other hand, some mobile arthropods in this study were probably underestimated. For example, big-eyed bugs (*Geocoris* sp.) were underestimated because they are able to detect an approaching observer and leave a plant before being counted. Hunting wasps (*Pemphredon* sp., *Psenulus* sp., and *Diodontus* sp.) were potentially important aphid predators in 1998, but their densities could not be estimated at all due to their extreme mobility. The number of plants surveyed in a sample varied with each experiment and is described with each experiment.

Experimental predator augmentation, 1997 and 1998: laboratory-reared lacewing larvae

In the 1997 and 1998 field seasons, the effects of a generalist predator in the field pea system were tested by augmenting larval lacewings (*Chrysoperla carnea* complex, following the nomenclature recommended by Tauber et al. 2000). One feature that makes *C. carnea* an attractive biocontrol agent is that it is native to North America.

Green lacewings are the most-purchased biological control insect, and *C. carnea* is recommended for application in field crops over other commercially-available lacewings (Tauber et al. 2000). However, lacewings are generalist predators and consume intraguild prey in some systems (Sengonca and Frings 1985). Subsequent observations confirmed that they attack IG prey in pea fields (Chang 1998, Chapter 2 of this dissertation).

The *C. carnea* colony was established in 1997 from green lacewings collected in Seattle, Washington. While *C. carnea* is relatively easy to rear in the laboratory, the difficulty of maintaining this colony for several generations eventually forced modifications in the experimental design. The colony began to decline during the 1998 field season. The decline caused a shortage of lacewings and reduced the number of treated plots in that year. The colony collapsed after the 1998 field season, possibly due to excessive inbreeding.

In 1997, 18-3 × 3 m experimental plots were planted in Sumner. Three of these plots acted as controls, while laboratory-reared lacewing larvae were added to the other 15 plots. Additional treatments involving the augmentation of a second natural enemy were abandoned due to logistical problems. Plot samples initially consisted of 4 randomly-selected plants in each plot. In later sampling, the number of plants inspected per plot was increased to 8, due to the large variation in insects seen from plant to plant. Four samples were taken from each plot, once per plot on July 16 (4 samples), July 21 (4), July 30 (8), August 6-8 (8), and August 18 (8).

In 1998, laboratory-reared lacewing larvae were experimentally released in randomly-selected plots at both sites. In Fife, 8-2 × 8 m plots acted as controls and 2-2 ×

8 m plots received lacewings. In Sumner, a smaller area was available for experimentation. Therefore, only 5-2 × 8 m plots served as controls and another 2 × 8 m plot was treated with lacewings. The unbalanced numbers of control versus treated plots were due to the collapse of the lacewing colony. In Fife, samples consisted of surveys of 8 randomly-selected plants, while in Sumner, a sample was 10 plants surveyed in a plot. Samples were taken on June 18, June 25, July 6, and July 20-21 in Fife, and on July 1, 9, 20, 30-31, August 7, and 13 in Sumner.

Lacewing larvae were released at densities between 1.1 to 2.2 larvae per m^2, as permitted by laboratory colony size. This density falls within the range of recommended release rates of commercial insectaries that sell juvenile lacewings (Table 3.1).

Experimental predator augmentation, 1999: tethered ladybird beetles

In 1999, following the collapse of the lacewing colony, I augmented populations of the seven-spotted ladybird beetle, *Coccinella septempunctata*. Like *C. carnea*, *C. septempunctata* is relatively generalized in its diet and engages in IGP in pea fields (Chapter 2). *C. septempunctata* was introduced into the U.S. by the Department of Agriculture for aphid control in the 1970s (Angalet et al. 1979) and has since become well-established in many parts of the country (Schaefer et al. 1987, Rice 1992, Elliot et al. 1996). *C. septempunctata* was the most abundant coccinellid in Sumner and Fife in 1997 and 1999, and the second-most abundant coccinellid in 1998.

Twelve 2 × 2 m pea plots established in Fife and four 2 × 5 m plots in Sumner were used for this experiment. At each site, half of the plots were randomly selected to be control plots. In the remaining plots, I augmented adult *C. septempunctata*. Because adult ladybird beetles are mobile and able to fly between the plots used in this study, I tethered them by their forewings using cyanoacrylate ("super glue"), fine wire, and thread. The augmented *C. septempunctata* were collected from vegetation separated by several meters of bare ground (tilled soil) from the experimental plots. Release rates ranged from 0.3 to 0.7 beetles per m^2. This density was primarily limited by the handling time I required for tethering the beetles.

For the 1999 experiments, 16 pea plants centered on a randomly selected point were sampled from each plot. Samples were taken from each plot in Fife once during five sampling periods: June 1 and 3, 7 and 10, 16 – 18, 23 and 24, and 29 – July 1. Each plot in Sumner was sampled once during five sampling periods: June 3, 15, 22, 28, and July 6 – 8. Two additional half samples (8 plants inspected) were taken in Sumner on July 15 and 22.

Assessing the impact of resident natural enemies

Parasitoids and fungi leave physical evidence of the aphid mortality that they cause. Pea aphids killed by parasitoids are called mummies and can be distinguished by their light brown color and greater roundness (Fluke 1929). Pea aphids that have been killed by fungus are called cadavers and are also visibly distinct from living aphids (Fluke 1929). In western Washington, most cadavers are pink to peach in color. The fungus gives the cadaver a fuzzy, bloated appearance compared to living pea aphids. A crude measure of the impact of parasitoids and fungal pathogens can be made by comparing the density of pea aphids to the densities of mummies and cadavers. A more precise measure of parasitoid- and fungal-induced aphid mortality can not be calculated because I do not have data on the relative life spans of aphids, mummies, and cadavers. Furthermore, the proportion of mummies and cadavers does not account for the action of predators. Predators will consume mummies and cadavers in addition to living pea aphids (Chapter 2).

I examined graphs of arthropod populations over time within growing seasons for evidence that natural enemies were tracking pea aphid populations. The numbers of living leaves, flowers, and pods on the pea plant were also plotted to reflect potential "bottom-up" (resource-driven: Hunter et al. 1997, Ylioja et al. 1999) influences in the pea field system.

Analysis of experimental augmentation

I used SYSTAT (1997) to perform a MANOVA to analyze the effect of predator augmentation in the experiments. Data were classified by experimental treatment (2 classes: control versus predator-augmented plots) and experiment (5 classes: Sumner 1997, Fife 1998, Sumner 1998, Fife 1999, and Sumner 1999). The response variables were the loads of pea aphids, herbivorous thrips, other herbivores, the sum of mummies (dead aphids containing developing parasitoids) and cadavers (dead aphids infected by fungi) as a group of specialist natural enemies, and predators as another intraguild group. The load of each group was calculated as an average for a plot of individuals per plant appearing in samples taken after predator augmentation treatments were applied. I stabilized the variance of the arthropod count data by adding 1 to each value and taking the logarithm prior to performing the MANOVA.

The variance of the number of prey on individual plants within predator-augmented plots and control was analyzed for the 1999 experiments with F-tests. Only the 1999 experiments were analyzed because unequal sample sizes in the other experiments make F-tests difficult to interpret.

Analysis of correlation among resident natural enemies

To assess the potential for IG encounters between resident natural enemies, I pooled the samples from treatment and control plots in the following analyses. To assess the interactions of resident natural enemies at the level of individual plants, I calculated a correlation matrix for several of the most abundant taxa in the three-year data set. Fungal pathogens, parasitoids, syrphid flies, spiders and coccinellids were the five natural enemy groups included in this analysis. Adult parasitoids and immature parasitoids contained in mummies were distinguished from each other. One reason for this is that adult parasitoids represent potential aphid mortality, while mummies reflect aphid mortality that has already occurred. Similarly, syrphids were classified by life stage as eggs, larvae, and pupae, to indicate potential, ongoing, and past sources of herbivore mortality. Coccinellid larvae and adults were grouped together in the analysis to increase their sample size and because both stages are predatory. Inactive coccinellid stages (eggs and pupae) were not abundant enough to warrant inclusion in this analysis. Herbivorous species for which correlation coefficients were calculated were pea aphids, bean aphids, all other aphids, thrips, and whiteflies. Correlation coefficients between arthropods and living leaves per plant were calculated to examine bottom-up influences.

Inspection of the correlation matrices indicated that natural enemy influences were likely to have been influenced by resources. Therefore, an apparent correlation between two natural enemies may reflect similar responses to resources such as pea aphid density. The effect of pea aphid density was statistically controlled by calculating partial correlation coefficients between natural enemies.

I then examined the net effect of all resident natural enemies on pea aphids at the level of plots. The dependent variable is the change in pea aphid populations between sampling periods. I used a 2 × 4 test of independence for categorical data to analyze the effect of natural enemy diversity on pea aphid population change. For each plot, pea aphid populations were classified as increasing, decreasing, or unchanged between consecutive sampling periods. To characterize natural enemy diversity, I categorized individual natural enemies into one of three types, fungi, parasitoids, and predators. Then the number of natural enemy types (from 0 to 3) in a plot during the first of the consecutive sampling periods was calculated.

Results

Impacts of resident natural enemies on pea aphids

For this analysis, treatment and control plots are combined because the predator augmentations had little detectable effect on the community (see next section). In the total study, I surveyed 2,546 pea plants. The average number of pea aphids, mummies, and cadavers per plant varied substantially from experiment to experiment. The average density of pea aphids was 3.77 per plant (n = 1160, SE = 0.23) in Fife and 8.81 (n = 1386, SE = 0.42) in Sumner. The densities of mummies and cadavers were much lower in Fife than in Sumner (Figure 3.2). In Sumner, the densities of aphids, mummies and cadavers varied temporally, both within and between years (Figure 3.3). In particular, 1999 had an unusually high density of aphids and cadavers (Figure 3.3c). In the Sumner 1999 experiment, the pea aphids began to decline as cadavers reached their highest density and while plant resources were declining (Figure 3.3 c and d).

Augmentation experiment results

The MANOVA found no significant effect of predator augmentation (Hotelling-Lawley trace = 0.053, $F_{5,36} = 0.382$, P = 0.858, Figures 3.4-8). Univariate F tests within the MANOVA did not find a significant effect on any of the individual dependant variables. Predator augmentation decreased pea aphid densities in four of the five experiments (Figure 3.4). However, the reduction in pea aphids was not large enough to make this a statistically significant result. Analysis of the individual experiments (where allowed by sample size) were consistent with the overall MANOVA and never found a statistically significant augmentation effect.

In contrast to the experimental predator augmentation treatments, the year and site in which an experiment was conducted had noticeably large and significant effects on the insect community (MANOVA: Hotelling-Lawley trace = 35.282, $F_{20,138} = 60.861$, $P = 9.992 \times 10^{-16}$, Figures 3.4-8). No two experiments are comparable in terms of densities of all five dependent variables. Instead, each experiment seems unusual in terms of at least one of the taxa (Table 3.2).

Augmented predators may have had an effect in the intra-plot variation in the number of prey on plants ("aggregation" in the phenomenological sense of Ives 1991).

In both of the 1999 experiments, the variance in the number of most likely prey per plant was lower in plots which received tethered seven-spotted ladybird beetles (Figure 3.9). This difference was statistically significant in the Fife 1999, but not the Sumner 1999, experiment (Fife: $F = 1.932$, $df = 227$, $P = 4.47\times10^{-7}$; Sumner: $F = 1.142$, $df = 31$, $P = 0.357$).

Correlation among residents

At the level of individual plants, most values for species abundance were zeroes. Even for the most abundant taxa, individuals were not normally distributed on plants. For example, nearly one-third of the pea plants sampled (811 out of 2546) were free of pea aphids, the most abundant taxon. Therefore, Pearson correlation coefficients between taxa (Appendix D) should be interpreted cautiously. Because of the great number of correlations analyzed, a Bonferroni correction was used to assess significance (SYSTAT 1997).

Both herbivores and predators were correlated with the number of green leaves on a plant (for example, whiteflies, syrphid larvae, thrips, and pea aphids, Table 3.3). The natural enemies that were significantly correlated with pea aphids were cadavers, parasitoids (in the form of mummies), and syrphid flies (in both the egg and larval stages). However, syrphid larvae were more strongly correlated with whiteflies and thrips (which were correlated with each other) than with pea aphids. Spiders were strongly correlated with thrips but not with any other herbivores. Certain natural enemies were positively correlated with each other. The strongest correlation occurred between cadavers and mummies. Other statistically significantly correlated pairs natural enemies were syrphid larvae and syrphid pupae, coccinellids and cadavers, and spiders and syrphid larvae. Even when the effect of pea aphid density is controlled by partial correlation, certain natural enemies remain strongly associated (Table 3.4).

The background density of resident natural enemies varied from plot to plot (Figure 3.8). Therefore, predators that were not experimentally augmented had the opportunity to influence prey densities. Pea aphid populations in plots in which natural enemies were present declined more often than populations in plots where no natural enemies were present (Figure 3.10), but this was not statistically significant (uncorrected $G = 2.76$, $df = 1$, $P = 0.10$, $n = 191$).

Substantial differences in arthropod community composition can be seen among years and between sites. Pea aphids reached their highest densities in 1999 (Figure 3.4), a year that was unusually cool and moist (Table 2.4). Also in 1999, the Sumner site contained an unusually high density of cadavers and mummies (Figure 3.7). Thrips reached exceptionally high densities in 1998 (Figure 3.5), when the months of July and August were hotter than most (Table 2.4). Resident predators show a similar but less pronounced pattern to thrips (Figure 3.8). The differences between sites and among years may contribute to the correlation between species at the level of plants.

Discussion

The goal of this study was to determine whether IGP by augmented generalist predators disrupts biocontrol in pea fields. Observations of cadavers and mummies in the field suggest that the amount of biocontrol provided by resident natural enemies varies with site and time (Figure 3.3). On average, resident natural enemies may have small, negative effects on pea aphids. Pea aphid populations increased less often in plots with higher natural enemy diversity (Figure 3.10). This trend might be stronger if an experiment could extract the positive correlation between numbers of natural enemies and pea aphids at the level of individual plants (Appendix D). The strongest impact of the natural enemy guild may be slowing the growth of large pea aphid populations rather than decreasing pea aphid populations.

An alternative interpretation of Figure 3.10 is that the presence of some natural enemies may decrease pea aphid populations, but having additional natural enemies may result in antagonism or disruption of control. IG victims in this study were parasitoids (as mummies), fungi (as cadavers), and syrphid larvae. The exploitative ability of the fungus can not be compared to the other natural enemies following the methods of Chapter 2. Thus, it is possible that the fungal pathogens (mostly *Pandora neoaphidis*) are relatively more-effective pea aphid enemies and are being disrupted by predators when both are concentrated in particular plots. Therefore, IGP could reduce the net effect of the guild at its highest level of diversity. However, this has not been tested. Laboratory work on ladybird beetles, *P. neoaphidis*, and pea aphids indicates that the beetles do not consume cadavers entirely and that uneaten fungal spores can be transported by beetles (Pell et al. 1997, Roy et al. 1998). It is possible, but as yet untested, that the enhanced transmission of the fungal pathogen by the ladybird beetles may produce synergistic effects between the two natural enemies in the field (Roy et al. 1998).

Separate experiments in which lacewings and ladybird beetles were augmented suggest that they do not disrupt biocontrol. However, predator augmentation did not markedly improve pea aphid control. The lack of effect of predator augmentation on the pea field community may be partially due to the inherent variability in the system, which made experimental effects within a particular year at a particular site difficult to detect. In addition, the experimental design was compromised by logistical difficulties in 1997 and 1998. The one species possibly affected by augmentation was the intended target pest, the pea aphid. Plots in which predators were augmented generally contained fewer pea aphids than control plots. Therefore, interference and IGP perpetrated by the augmented predators did not disrupt whatever level of biocontrol is provided by the resident natural enemies in the system.

Existing IGP theory can explain why augmenting IG predators did not disrupt biocontrol in this system. Actively foraging IG predators and IG victims are equally effective exploiters of pea aphids, and IGP occurs in proportion to the abundance of IG prey (Chapter 2). Several general models predict that disruption will not occur under these conditions (Hassell 1978, Polis et al. 1989, Polis and Holt 1992, Schreiber and Gutierrez 1998). It is important to remember that IGP will not always disrupt biocontrol and that adding generalist predators to a system can still improve biocontrol even if they kill a few IG prey. Most reports of IGP do not examine its consequences on shared prey (pest) populations (Rosenheim et al. 1995 and Figure 3.1). As often as not, studies that extend to the population level find that IG predators can improve biocontrol (Rosenheim et al. 1995 and Chapter 1). Therefore, the automatic labeling of an IG predator as a "good bug gone bad" (paraphrased from Kester and Jackson 1996) is not justified.

It is possible to make a general recommendation to avoid IG predators for biocontrol on reasoning from stability analysis of models and evolutionary arguments. Over the long-term, in models of IGP based on modified Lotka-Volterra equations, an IG victim can only coexist with an IG predator when the IG victim is more effective at utilizing the shared prey (Polis et al. 1989). If the IG victim is more effective at prey exploitation than the IG predator, then the inclusion of the IG predator in the system will increase the density of the shared prey. Therefore, in agricultural systems where IG predators and IG prey have coevolved, IG predators disrupt biocontrol.

For the above reasoning to hold, at least two conditions must be met. First, the species in the community must interact for a period of time long enough to reach ecological stability. Second, the interactions of the IG predator, IG prey, and shared prey must be the primary determinant of their ability to coexist. Pea fields may violate both of these conditions. Peas have been grown in Washington state for over a century (Severance 1911). Insects have the potential to evolve within such a period of time (Huey et al. 2000), but some additions to the community have occurred fairly recently. In particular, *C. septempunctata* became established in Washington state only between 1987 and 1990 (Rice 1992). It is difficult to find evidence for the pea community being ecologically stable. Furthermore, it is unlikely that coexistence in pea fields is entirely determined by interactions within the field boundary. For example, I observed several of the natural enemy species as well as pea aphids in habitats other than peas. These range from old grass fields (with clover, *Trifolium* spp., hosting the pea aphid) to beach areas (where beach pea, *Lathyrus japonicus*, was the host plant for the pea aphid).

Additionally, since pea is an annual crop, it is also likely that overwintering conditions would influence any long-term coexistence.

While theory provides one explanation for the lack of disruption of pea aphid control by IGP, it is possible that for the other herbivore populations, the high variability in this system at the level of plots may have masked disruption (Figures 3.5 and 6). The variability at the level of plots may have been due to their layout in relationship to the surrounding landscape. Although treatments were assigned randomly, the Sumner site in particular may have lacked the replication to overcome the variation induced by proximity of each plot to different habitats (described further below). Rare events may have also contributed to plot-level variability. As an anecdotal example, in 1997 a single frog (probably *Hyla regilla*) was found in one of the plots in Sumner. While this frog was not observed interacting with any of the arthropods in the plot, its relatively large biomass may have allowed it to consume many individual prey the size of an aphid. Similarly, other relatively large vertebrates such as crows, killdeer, and dogs were able to enter plots freely.

The variability among years and between sites was factored into the statistical analysis, but is itself interesting to consider. Two of the substantial factors contributing to differences among experiments were weather and landscape. The three years of this study contained an El Niño event (1998) and a La Niña event (1999). The result was that for the months of June and July, 1998 was atypically hot and dry, while 1999 was unusually cool and wet (Chapter 2, Table 2.4). The weather probably contributed to the unusually high abundance of hunting wasps in 1998 (Chapter 2) and pea aphids in 1999 (Figure 3.4).

The fungal pathogen also reached unusually high densities in 1999, but only at the Sumner site (Figure 3.7). Many arthropod groups were more abundant at the Sumner site, the one notable exception being spiders (especially in 1998; note the abundance of "other predators" in Figure 3.8). The landscape surrounding the two sites may help explain why they differ in community composition. The Sumner site was surrounded by agricultural and fallow fields, and within meters of a residential road. The Fife site was adjacent to a light industrial and commercial zone, as well as agricultural fields. The Fife site was also within several meters of a heavily-used road that may constitute a substantial mortality source for a variety of insects (Hostetler 1997). (Incidentally, traffic by the Fife site is so heavy that the Washington State Department of Transportation is extending a highway through the farm.)

Avoiding disruptive IGP is necessary but not sufficient to improve biocontrol. The augmentation treatments only marginally improved pea aphid control. This may be because IGP, while not disruptive, decreases the amount that each additional individual natural enemy can affect pea aphid populations. In other words, IGP may impose diminishing returns on predator augmentation. Another limit on predator impact may be the defensive behavior of pea aphids. The main response of pea aphids to attacks by relatively large predators (such as lacewings and ladybird beetles) is to flee, often by dropping from the host plant (Evans 1976). Of pea aphids physically contacted by lacewing larvae and adult seven-spotted ladybird beetles, 53.4% escaped being eaten (Chapter 2). Similar escape values for pea aphids have been observed in other systems (Evans 1991). The number of pea aphids that move in response to the presence of a predator is larger than the number that are contacted, because attacked pea aphids release an alarm pheromone that causes conspecifics to engage in escape behaviors (Dill et al. 1990). Therefore, many more individual pea aphids may leave the vicinity of a foraging predator than are consumed by the predator. If predators concentrate their attacks on aggregations of pea aphids, then the behavioral response of the aphids may spread their population more evenly among plants within the traveling ability of individual aphids (Frazer 1977, Roitberg et al. 1979, and Figure 3.9). The implications of pea aphid redistribution for pea plants are not clear. A more even distribution of aphids may improve conditions for pea plants, because plant damage is a sigmoidal function of pea aphid density (Yencho et al. 1986). However, pea aphids sometimes transmit a plant virus, so increased aphid spread could increase disease among plants (Frazer 1977).

Another question that remains unanswered is whether biocontrol by native or established natural enemies of the pea aphid can be improved further. Several general, compatible methods have been suggested for improving conservation biocontrol (Speight 1983, Lewis et al. 1997, Barbosa 1998, Bottrell et al. 1998). Two factors that are involved are increasing the number of natural enemies and increasing the effectiveness of natural enemies. Increasing the number of augmented biological control agents to extremely high densities may improve pea aphid control, depending on the whether and to what extent IGP and interference impose diminishing returns. Field cage examples of successful augmentative biological control using lacewings released them at densities of 6 to 74 larvae per square meter (Ridgway and Jones 1968, Ridgway and Jones 1969), much higher than the release rates in this study, and even higher than commercial recommendations (Table 3.1). However, a practical consideration is the economic cost involved with augmentative biological control, especially with the possibility of diminishing returns. The price of pest control will likely matter to the typical farmer in the United States who faces severe economic challenges (National Commission on Small Farms 1998). A preliminary search of insectaries on the Internet reveals that the cost of lacewings for augmentation is highly variable (Table 3.5). In some cases, lacewings are less expensive than an approximately equivalent dose of insecticide. However, the cost of lacewings usually greatly exceeds the cost of insecticide. Effort could be put into augmenting potentially more-effective natural enemies. Behavioral observations of foraging predators and distribution of prey on individual plants suggest that leaf surfaces constitute a relative refuge for pea aphids from both lacewings and ladybird beetles (Chapter 2). Other natural enemies, such as syrphid larvae and hunting wasps, are more capable of foraging on leaf surfaces and might provide a greater amount of pea aphid control when augmented. However, syrphids and hunting wasps are both more difficult to rear in the laboratory than lacewings or ladybird beetles. I had difficulty merely keeping hunting wasps alive in the laboratory for more than 48 hours. For an open field setting, habitat modification may be the most practical way to increase natural enemy populations.

I know of only one example involving peas in which different habitats were compared to determine which was more favorable for natural enemies (Peng et al. 1993). That study was performed in England, and compared the arthropods associated with peas in monoculture to those in a diversified system. In the diversified system, alleys of peas were planted between rows of furniture-timber trees. On average, the natural enemy population was 11% higher in the diversified system. The pest population consisted mostly of thrips and was 5% lower in the diversified system. Thus, habitat modification can improve biocontrol in peas by increasing natural enemy densities, although practical applications will depend on site-specific characteristics (Altieri 1999).

Much of the site-specific biological information required to improve biocontrol through habitat modification is missing for many crops (Ferro and McNeil 1998, Landis and Menalled 1998) including peas. A considerable body of general knowledge exists to guide particular efforts to enhance natural enemy populations (Barbosa 1998, Altieri 1999). For example, diversified systems (as is Peng et al. 1993) can provide food and shelter that boost natural enemy densities (Root 1973, Barbosa and Wratton 1998, Ferro and McNeil 1998). The spatial arrangement of crops can also be modified to improve the mobility of natural enemies (Kareiva 1990). However, the resource preferences for some natural enemy species may be incompatible (Banks 1999). In the current study, spiders and fungal pathogens may be an example of two groups with incompatible habitat requirements. During the entire study, spiders were most abundant in 1998 at the Fife site, while cadavers were most abundant in 1999 at the Sumner site. If the differences in the abundance of the two groups is due to physiological reasons rather than chance, it may not be possible to enhance the habitat for one group without worsening it for the other.

Finally, it may be possible to increase predator effectiveness by altering features of the pea plant. Pea mutations that decrease leaf surface area (Kareiva and Sahakian 1990) and surface wax (Eigenbrode et al. 1998) have both increased the effectiveness of particular predators foraging for pea aphids. However, modifying traits sometimes incurs an agronomic cost to the pea plant, such as increased risk of desiccation (Eigenbrode pers. comm.). Future progress toward effective conservation biocontrol in peas and other crops may require combining all of the efforts surveyed above.

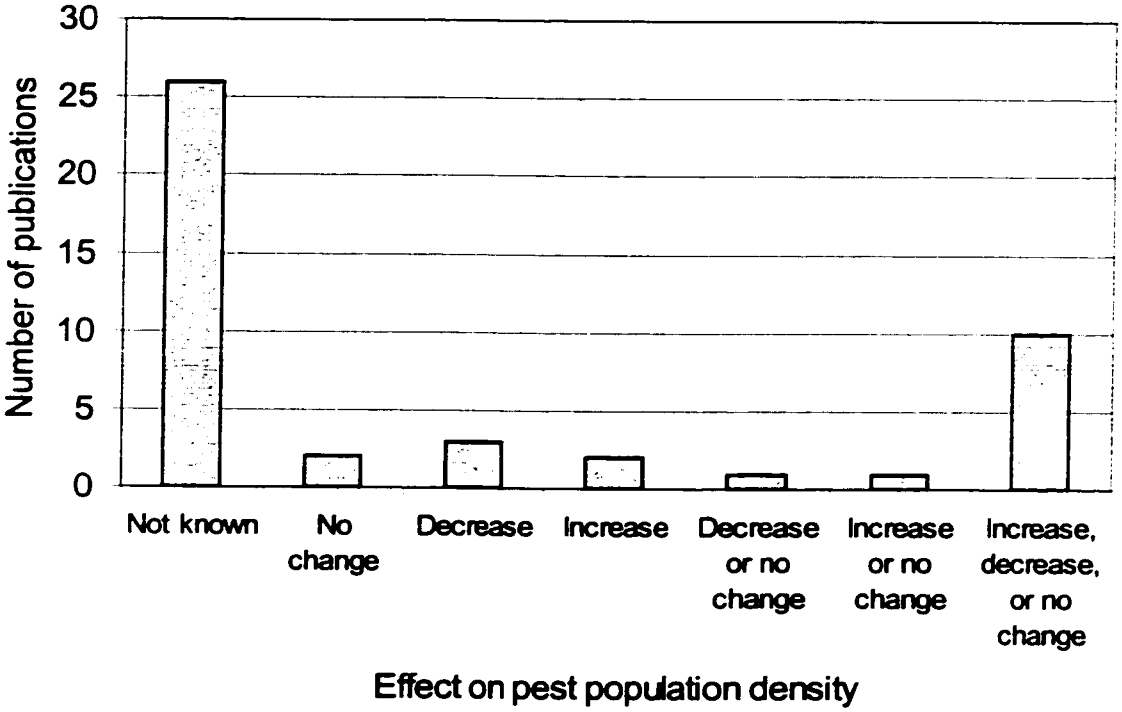


Figure 3.1 Summary of Rosenheim et al.'s (1995) review of intraguild predation involving predators of arthropods. Rosenheim et al. selected 45 publications describing IGP in biocontrol systems. The effect of including the intraguild predator on target pest density was determined in less than half of these studies. In the remaining studies, all possible outcomes were found. In most of the studies that examined population-level consequences of IGP, the addition of the IG predator increased and decreased pest densities in the same study.

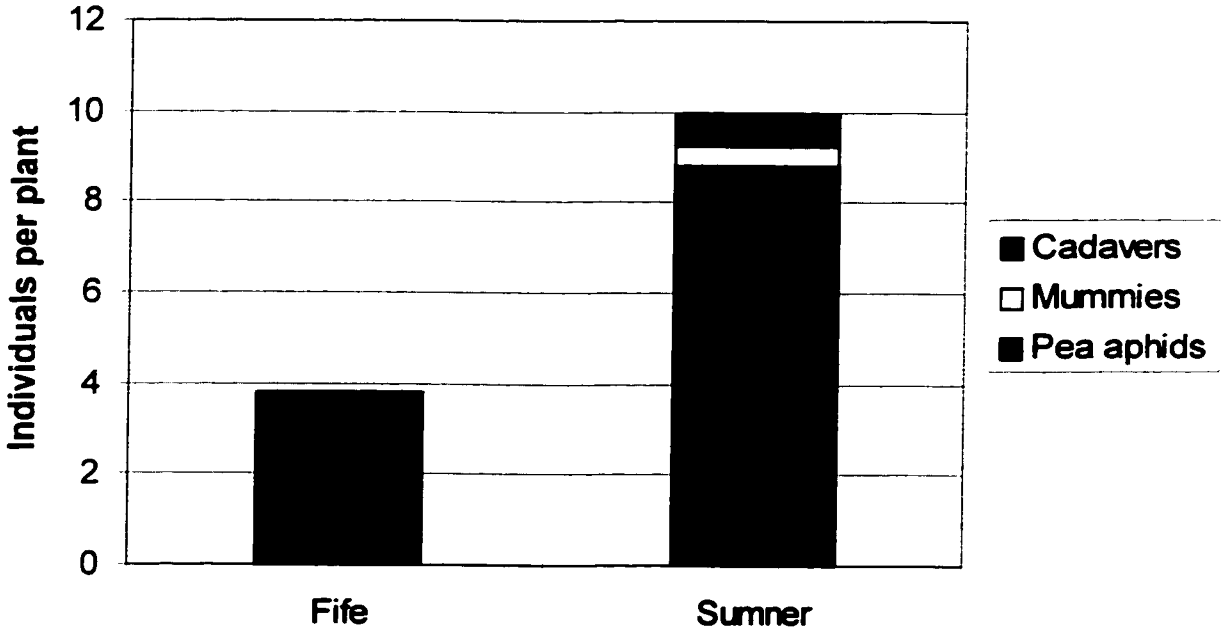
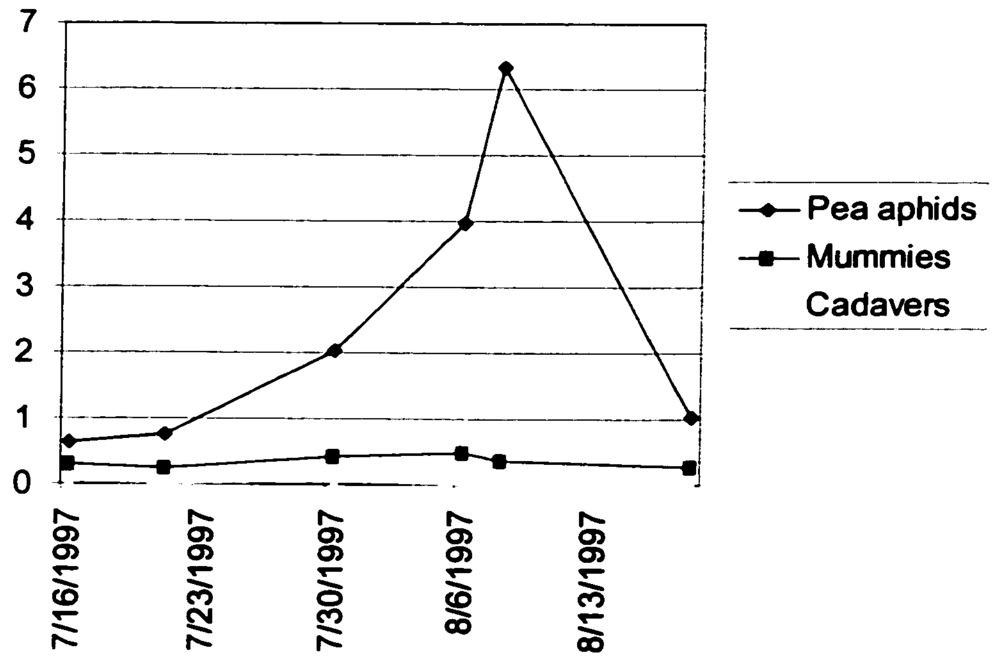
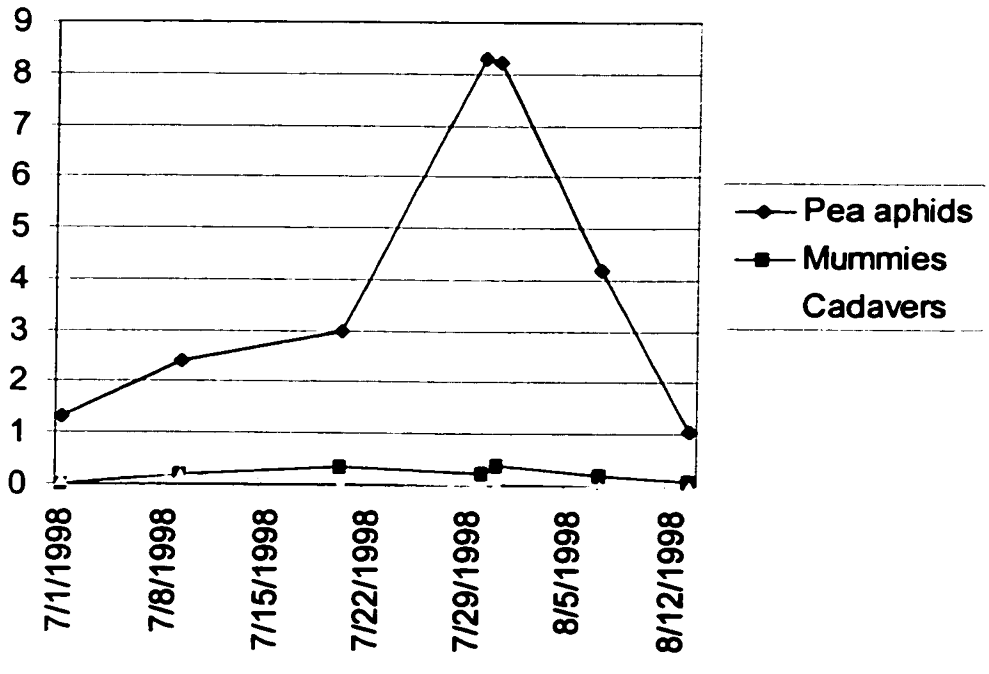


Figure 3.2 Average density of pea aphids, cadavers, and mummies by site for all sampling periods. The values for cadavers and mummies in Fife are too low to appear on this graph (0.0095 and 0.035 individuals per plant, respectively).

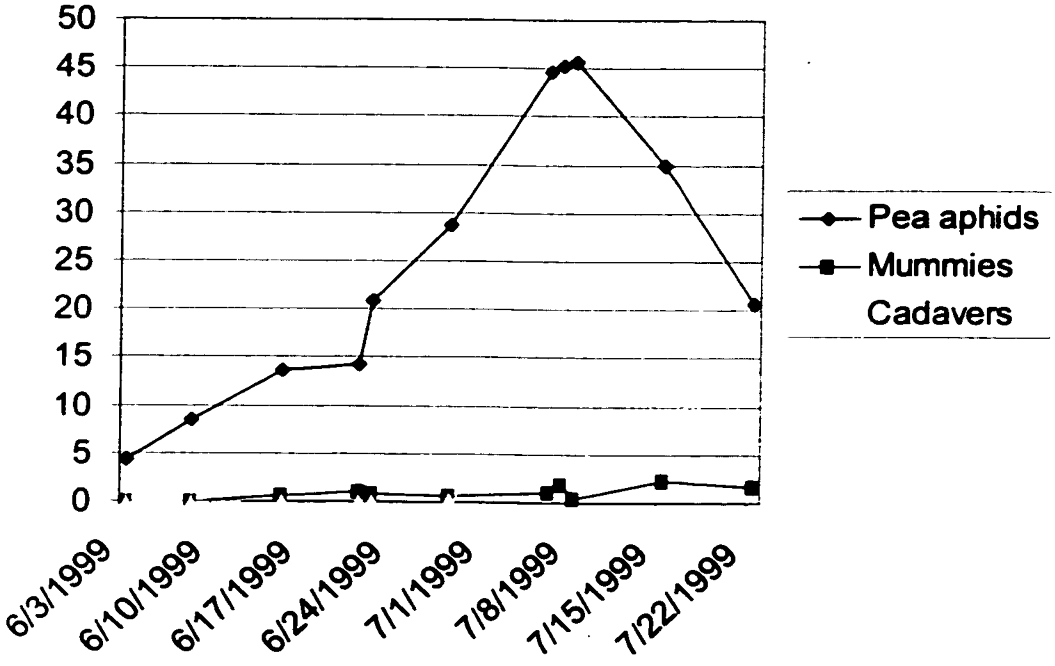
a.


7
6
5
4
3
2
1
0
7/16/1997
7/23/1997
7/30/1997
8/6/1997
8/13/1997
Pea aphids
Mummies
Cadavers

b.


9
8
7
6
5
4
3
2
1
0
7/1/1998
7/8/1998
7/15/1998
7/22/1998
7/29/1998
8/5/1998
8/12/1998
Pea aphids
Mummies
Cadavers

c.



d.

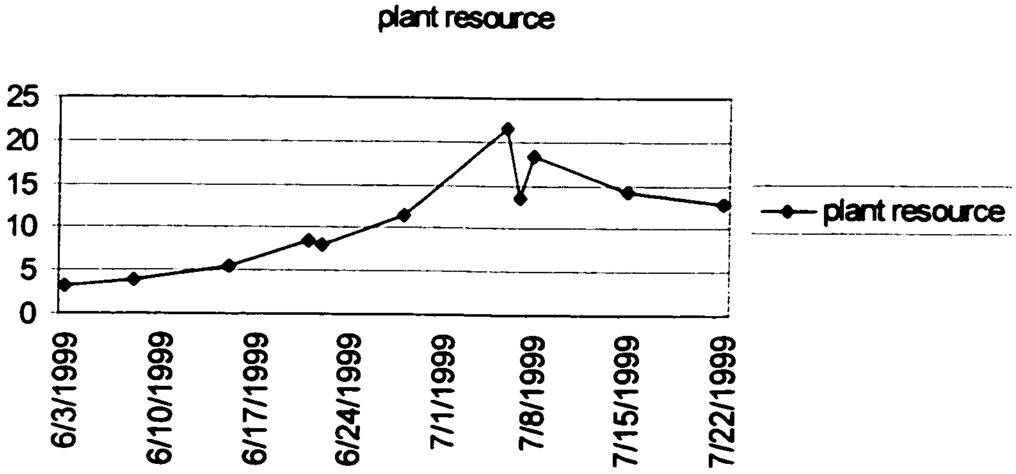


Figure 3.3 Comparisons of pea aphid, mummy, and cadaver densities in the Sumner 1997, 1998, and 1999 experiments (a, b, and c, respectively).

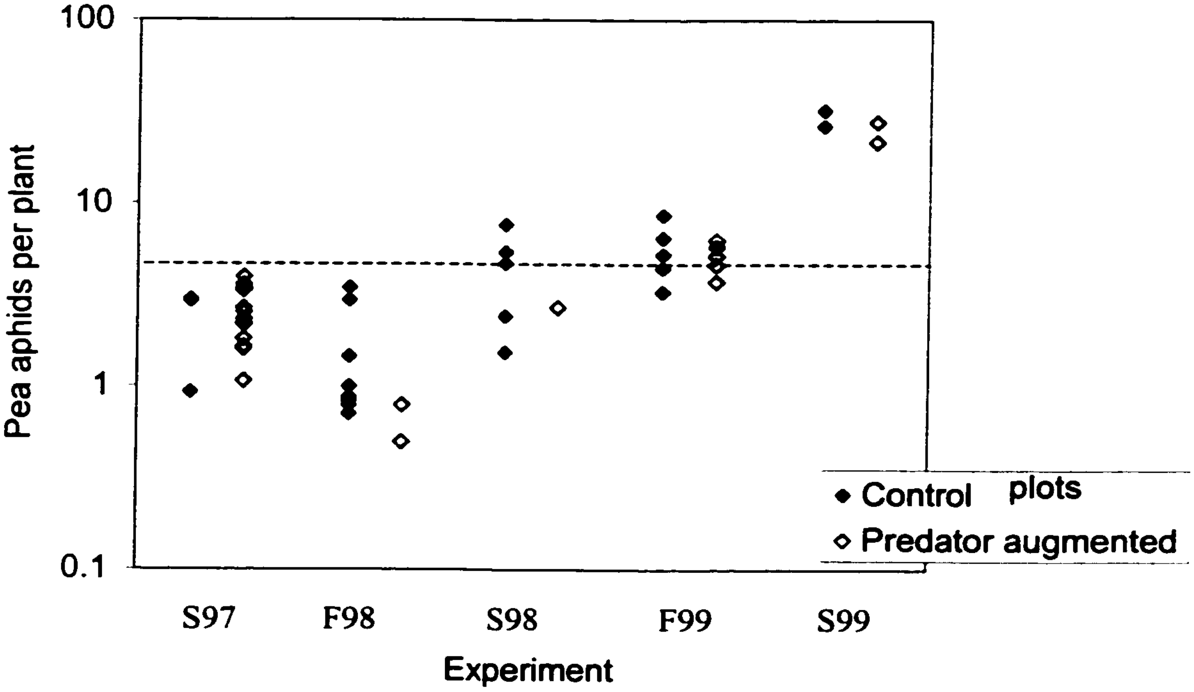


Figure 3.4 Response of pea aphids to predator augmentation and experiment. Dashed line represents the unweighted average number of pea aphids per plant for all plants surveyed. The dependent variable of pea aphid load is the average number of aphids per plant in samples taken after augmentative releases. The number of plots in each experiment was (numbers of control and treated plots): Sumner 1997 (3, 15); Fife 1998 (8, 2); Sumner 1998 (5, 1); Fife 1999 (6, 6); Sumner 1999 (2, 2). Pea aphids declined in response to predator augmentation in four of the five experiments, but this was not statistically significant. Sumner may be a better site than Fife for pea aphids. The pea aphid density was much higher in Sumner in 1999 than in any other experiment (note logarithmic scale).

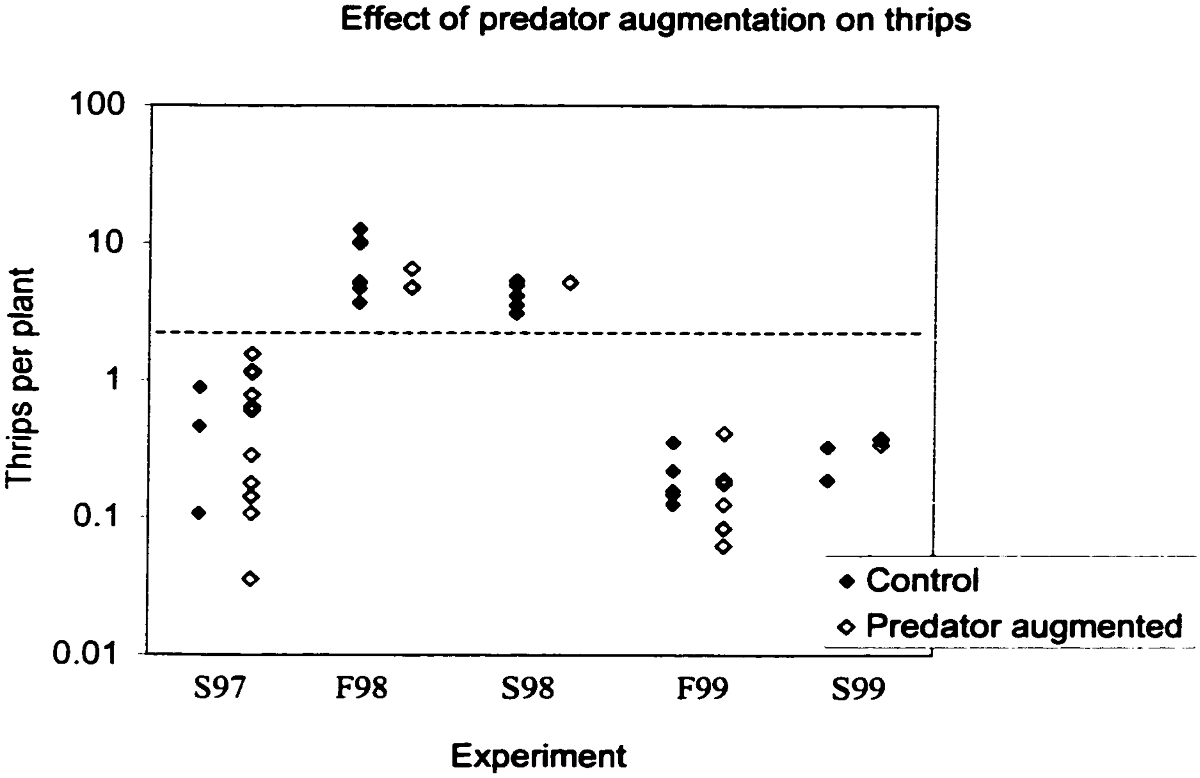


Figure 3.5 Response of thrips to predator augmentation and experiment. Format follows Figure 3.4. The 1998 growing season was particularly good for thrips, as densities were an order of magnitude higher that year than in 1997 or 1999 (note logarithmic scale). No difference by site or by predator treatment is apparent.

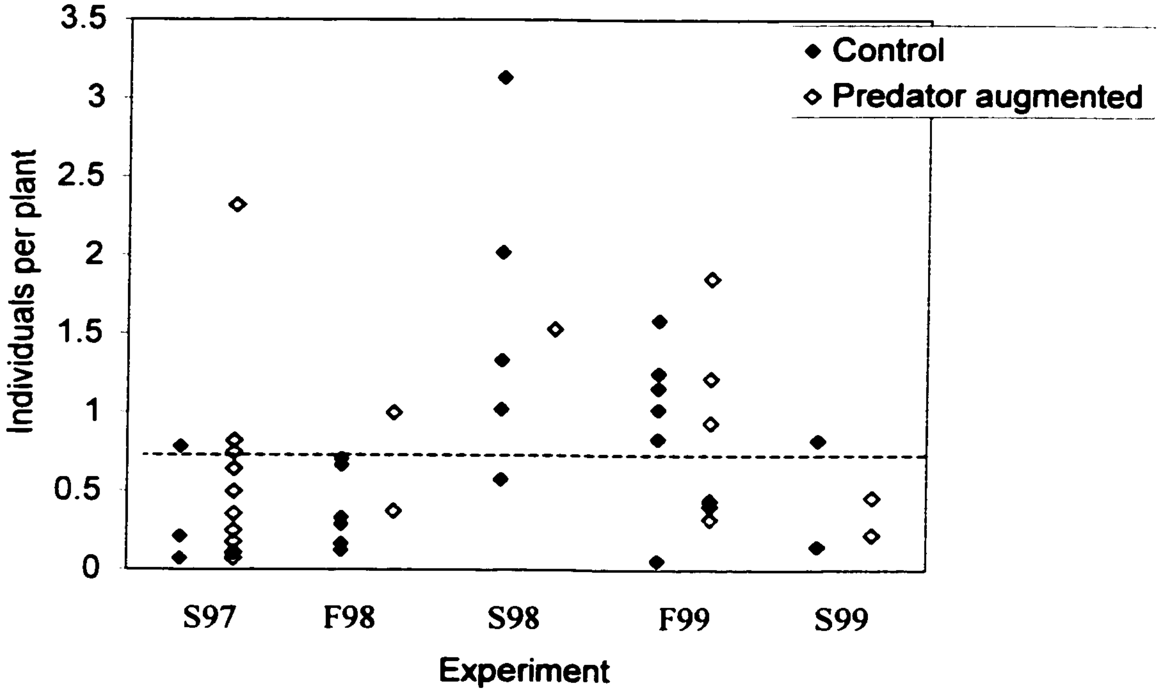


Figure 3.6 Response of miscellaneous herbivores to predator augmentation and experiment. Format follows Figure 3.4. The group of miscellaneous herbivores consists of all herbivorous arthropods that are not pea aphids or thrips (see Appendix C). No response to predator augmentation is apparent. Particularly high densities were seen in Sumner 1998 and to a lesser extent in Fife 1999.

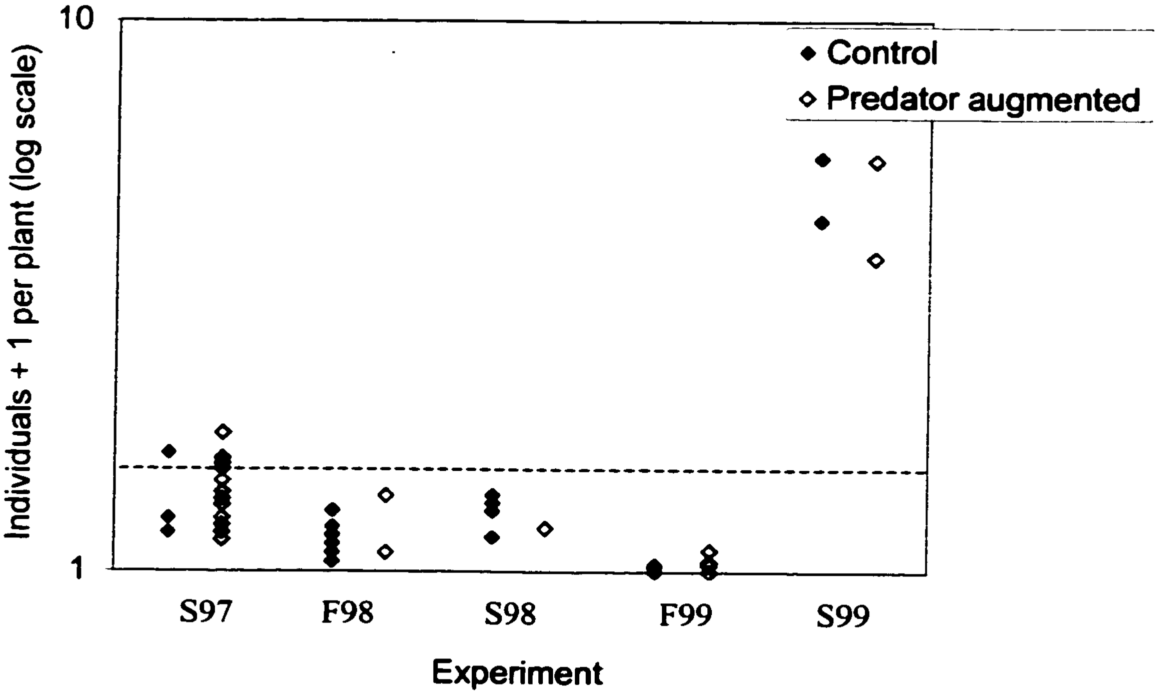


Figure 3.7 Response of the most likely victims of intraguild predation, fungi and parastoids, to predator augmentation and experiment. Format follows Figure 3.4. Parasitoid and fungus density shows little response to predator augmentation. A striking difference can be seen in 1999. In that year, the fungal pathogen *Pandora neoaphidis* killed many pea aphids at the Sumner site, but failed to have an outbreak at the Fife site.

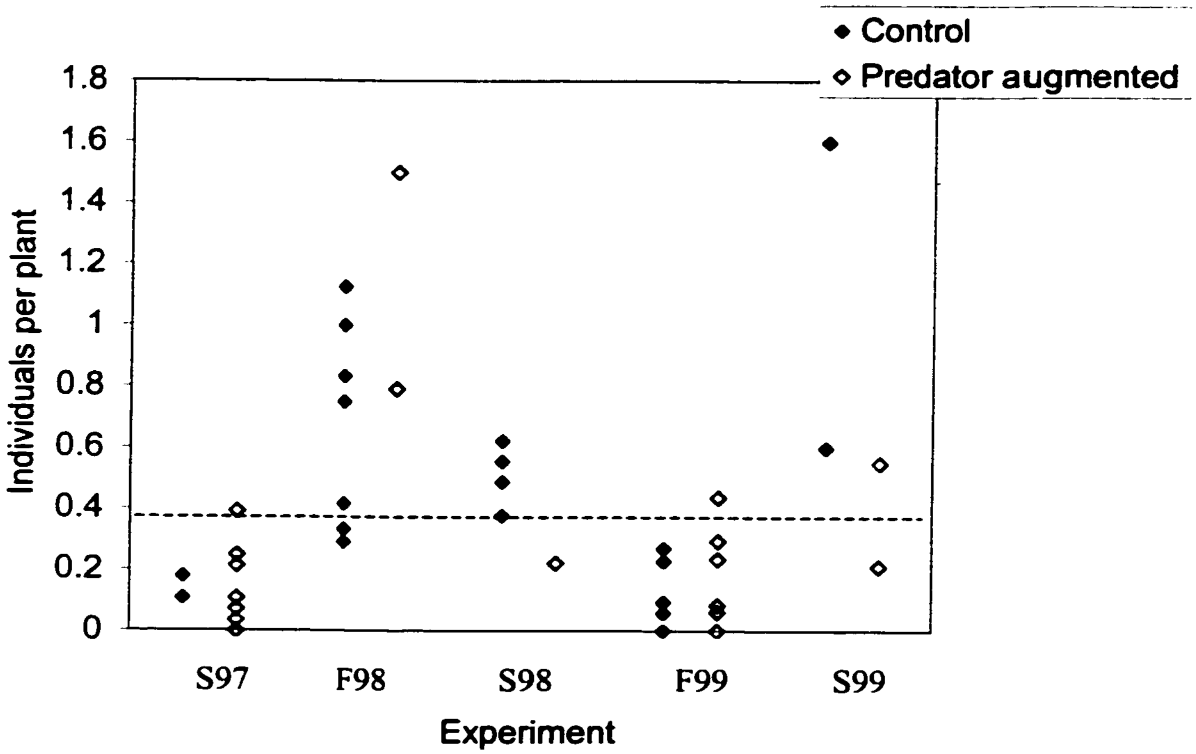


Figure 3.8. Response of resident predators to predator augmentation and experiment. Format follows Figure 3.4. For a list of resident predator taxa, consult Appendix C. Predator augmentation had little effect of the density of resident taxa.. Resident predators were particularly abundant in Fife 1998 and Sumner 1999.The most abundant predators in Fife 1998 were spiders, while the most abundant predators in Sumner 1999 were syrphids.

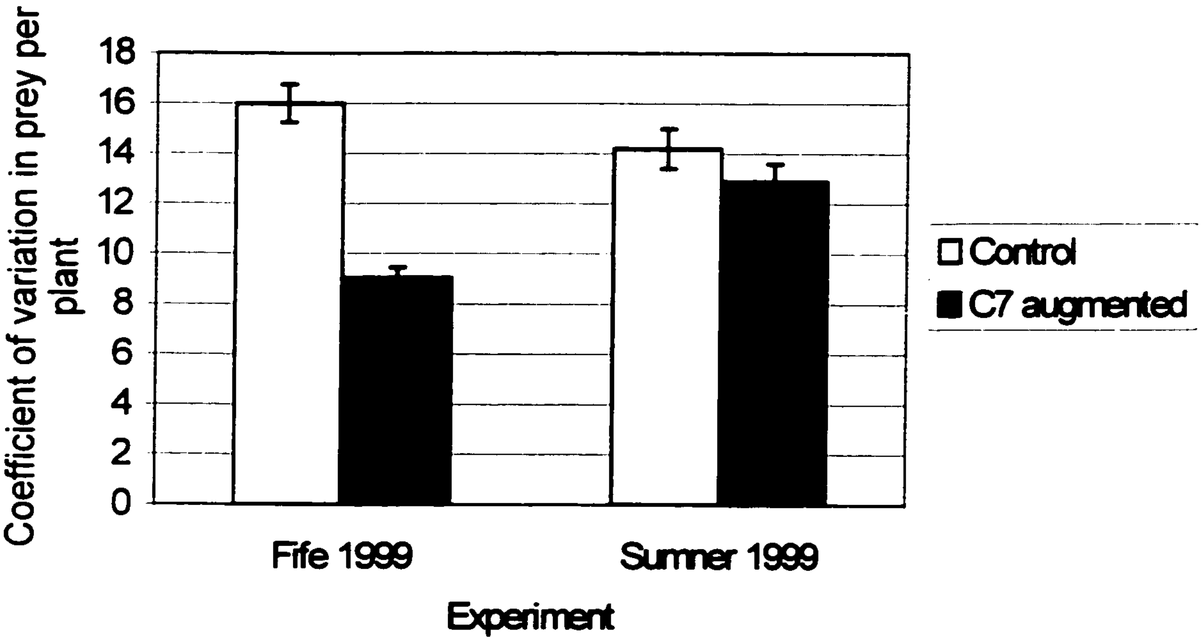


Figure 3.9 Effect of tethered ladybird beetles on aggregation of prey at the scale of individual pea plants. Bars represent standard errors.

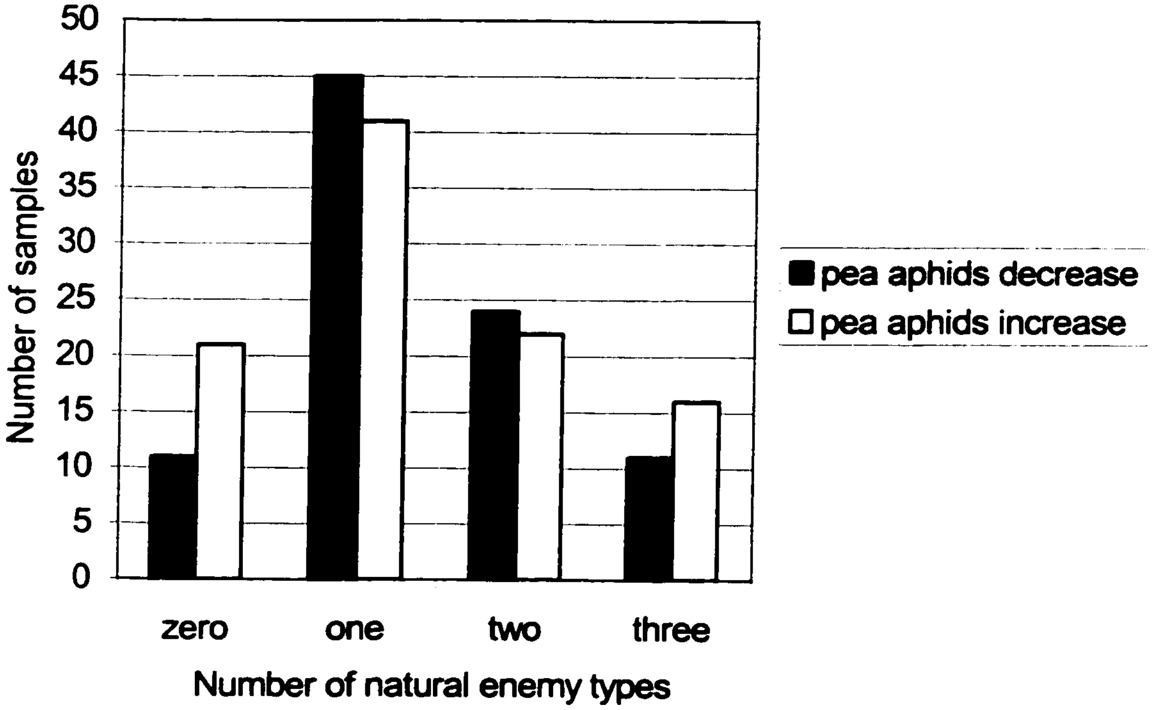


Figure 3.10 Relationship between pea aphid population changes and number of natural enemy types in a plot.

Table 3.1 Commercially recommended release densities for lacewings as biological control agents. "Density" is the recommendation for eggs per square meter except in two cases where larvae are noted. Recommended release densities for larvae are tend to be lower than for eggs because of increased survival of larvae. Larval releases are also more effective than egg releases in some cases (Tauber et al. 2000). However, the price of larvae is 3 – 4 times greater than the cost of eggs. Only three insectaries provide larvae. Mention of a supplier does not imply any form of endorsement.

Insectary	Density	Notes
A-1 Unique Insect Control	21.5	in greenhouses
A-1 Unique Insect Control	1.2	in field
Agralan Garden Products	4.0	as larvae
Arbico	53.8	presumably in greenhouses
Arbico	2.5 - 12.4	presumably in the field
Arizona Biological Control	53.8	presumably in greenhouses
Arizona Biological Control	2.5 - 12.4	presumably in the field
Beneficial Insectary	"relatively low"	
Bug Store	10.8	
Buglogical Control Systems	53.8	
March Biological	10.8	eggs or larvae, repeat as necessary
Nature's Control	1.2 - 12.4	repeat as necessary
Nature's Control	0.2 - 1.2	as larvae; repeat as necessary

Table 3.2 Summary of unusually high and unusually low densities of particular arthropod groups by experiment. While the location of the experiment in space and time had strong effects on arthropod community composition, effects of individual sites and years could not be determined. In other words, I cannot say that a "Fife effect" exists unless I specify an individual year. See text for explanation of the experiments and arthropods involved.

	Sumner 1997	Fife 1998	Sumner 1998	Fife 1999	Sumner 1999
pea aphids		↓			↑
thrips		↑	↑	↓	↓
other herbivores			↑		
intraguild prey				↓	↑
predators	↓	↑		↓	↑

Table 3.3 Summary of correlation coefficients at three spatial scales (See Appendix D).

	Leaves	Pea aphids	Thrips	Bean aphids	Other aphids	Whiteflies	Cadavers	Parasitoids	Mummies	Syrphid eggs	Syrphid larvae	Syrphid pupae	Spiders
Pea aphids	AC												
Thrips	AC												
Bean aphids													
Other aphids	ACD		AC										
Whiteflies	ACD		ACD		ACD								
Cadavers	AC	ACD	B	D									
Parasitoids													
Mummies	AC	ACD		C			ACD						
Syrphid eggs		A											
Syrphid larvae	ACD	AC	AC			AC							
Syrphid pupae	AC		ACD		A	CD					AC		
Spiders	AC		AC										
Coccinellids		AC					ACD		CD				

A = statistically significant positive correlation after Bonferroni correction for multiple comparisons at the plant scale.
B = statistically significant negative correlation after Bonferroni correction for multiple comparisons at the plant scale.
C = statistically significant positive correlation after Bonferroni correction for multiple comparisons at the plot scale.
D = statistically significant positive correlation after Bonferroni correction for multiple comparisons at the farm scale.

Table 3.4 Partial correlation coefficients with pea aphids as the control variable compared to multiple correlation coefficients for pairs of natural enemies. Correlation coefficients and partial correlation coefficients were calculated at the plot level.

Natural enemy species	**Correlation coefficient**	**Partial correlation**
Cadavers and mummies	0.68	0.52
Cadavers and coccinellids	0.59	0.52
Coccinellids and mummies	0.40	0.28
Syrphid larvae and pupae	0.25	0.28
Syrphid larvae and spiders	0.18	0.23
Syrphid larvae and cadavers	0.10	-0.13
Syrphid larvae and mummies	0.10	-0.06
Syrphid larvae and parasitoids	0.10	0.11

Table 3.5 Advertised prices of pest controls on the Internet. The search engine "Metacrawler" (Go2Net.com 2000) was used to find suppliers of biological and chemical pest controls. I searched for "green lacewings" on March 9, 2000 and "Cygon" on July 2, 2000. Interestingly, this search method found more insect than chemical suppliers. The price per area treated was calculated based on the suppliers' recommended application rates when provided online. Mention of a product or supplier does not imply any form of endorsement.

Type of control	Price per unit	Cost per 1000 ft^2 treated	Supplier and Internet address
Green lacewing	not available	not available	A-1 Unique Insect Control, http://www.a-1unique.com/products.html
Green lacewing	£ 7.99 per 20 larvae	varies with exchange rate	Agralan Garden Products, http://www.cf.ac.uk/insect/pesteat.html
Green lacewing	\$3.45 - \$7.75 per 1,000 eggs	\$0.79 - \$38.75	Arbico- http://www.biconet.com/biocontrol/lacewing.html
Green lacewing	\$6.75 per 1,000 eggs	\$1.55 - \$33.75	Arizona Biological Control, http://www.ethicalshopper.com/world_mall/home/garden/arb_1100_lacewing.htm
Green lacewing	not available	not available	Beneficial Insectary, http://www/theinsectary.com/lw/lacewing.htm
Green lacewing	\$3.20 - \$6.50 per 1,000 eggs	\$3.20 - \$6.50	Bug Store, http://www.bugstore.com/_private/lacewing.html
Green lacewing	\$2.78 - \$8.95 per 1,000 eggs	\$13.90 - \$44.75	Buglogical Control Systems, http://www.gardeninsects.com/grnlace.shtml
Green lacewing	\$6.00 per 1,000 eggs, \$21.00 per 1,000 larvae	\$6.00 - \$21.00	March Biological, http://www.marchbiological.com/L/green_lacewing.html
Green lacewing	not available	not available	Nature's Control, http://www.naturescontrol.com/three.phtml
Dimethoate (Cygon)	\$9.95 per pint	not available	Muncy's Rose Emporium, http://www.flsuncoast.com/muncyrose/
Dimethoate (Cygon)	\$10.79 per pint	not available	RidaBug.com, http://www.ridabug.com/
Dimethoate (Cygon)	\$44.70 per gallon	\$1.79 - \$3.58	United Spray Systems, Inc., http://www.bugpage.com/uss.html
Dimethoate (Cygon)	\$11.50 per pint	not available	Do it yourself Pest Control, Inc., http://doyourownpestcontrol.com/

Chapter 4

Synthesis and future directions in understanding and utilizing natural enemy guilds for biological control

Major findings of the previous chapters

- Several agroecosystems contain multiple species of natural enemies attacking the same pest(s) (Chapter 1).
- The community-level consequences of interactions between natural enemies are variable but can be understood with mechanistic information, such as where different natural enemies forage and whether they are likely to eat each other in addition to the target pest (Chapter 1).
- Natural enemies of the pea aphid in western Washington have different foraging patterns in space and time (Chapter 2).
- Mathematical models of intraguild predation predict that it can disrupt biological control when intraguild victims are better exploiters than intraguild predators, or when intraguild victims are the preferred prey of intraguild predators (Chapter 2).
- The exploitative ability of intraguild predators and intraguild victims is equivalent when their kill rates of pea aphids are compared (Chapter 2).
- Natural enemies do not prefer intraguild prey to pea aphids (or vice versa) (Chapter 2).

- The composition of the natural enemies in the system varied considerably from year-to-year (Chapter 2).
- Augmentation of intraguild predators does not disrupt the biological control of pea aphids by resident natural enemies (Chapter 3).
- Augmented natural enemies spread pea aphid populations more evenly among individual pea plants (Chapter 3).
- Intraguild predation between resident natural enemies does not seem important in limiting their impact on pea aphid populations (Chapter 3).

Contributions of the preceding chapters

I hope that I have clarified the connection between the behavior of intraguild predation and population-level patterns of the pea aphid. I worked in an open field setting and tried to incorporate all of the potentially interacting species, which is unusual in studies of intraguild interactions. I deliberately chose to work in open plots in order to generate results that could be directly related to situations faced by farmers. However, the variability in the system weakened the population-level findings. Still, the applied message is that even though lacewings and ladybird beetles attack other natural enemies in pea fields, they may still be augmented without disrupting the level of biocontrol provided by resident natural enemies.

The behavioral results support existing IGP theory but also illustrate areas where it may still progress. In particular, some IGP theory predicts that only exploitatively-superior intraguild victims can coexist with intraguild predators in the long-term (Polis et al. 1989, Polis and Holt 1992). However, many crops contain species that have interacted for only a short time on an ecological time scale. Furthermore, the long-term coexistence of organisms in annual and other highly-disturbed crop fields may be more closely related to interactions beyond the crop habitat. Therefore, results from equilibrium analyses may not be completely adequate for explaining the consequences of IGP in many annual crop systems.

A few future directions

Practical improvements of biological control of pea aphids will most likely depend on increasing the density or effectiveness of natural enemies in pea fields. For example, natural enemy populations in pea plots can be increased by planting them next to certain trees (Peng et al. 1993). Varieties of peas are available that improve the ability of natural enemies to grasp the plant and encounter prey (Kareiva and Sahakian 1990, Eigenbrode et al. 1998). Unexpected consequences from efforts to increase the density or effectiveness of natural enemies may arise that can be understood by paying attention to intraguild interactions. Habitat modifications and crop varieties that alter the encounter rate between natural enemies and pests may also alter the encounter rates of natural enemies with each other.

One direction for future theoretical work involves investigations of population dynamics in ephemeral crops. Simulation models (such as those by Gutierrez et al. 1984, Gutierrez et al. 1990, and Gutierrez 1992) may be useful in identifying the short-term population dynamics that deviate from equilibrium expectations. I have begun working on a simulation based on the pea field system (Appendix E) that suggests that IGP may improve biocontrol under certain rare conditions. During the early part of the growing season, IGP may be important in maintaining populations of natural enemies when pest densities are low. Keeping more natural enemies in a field early in the season may provide better preventative pest control.

The complexity of actual agroecosystems presents enormous empirical challenges. Interaction matrices of natural enemies would allow workers to distinguish between IG predators that are disruptive to a single other natural enemy and those that are disruptive to multiple natural enemies. In a caged experiment involving two natural enemy species, a disruptive interaction would seem disastrous to biological control. However, in a real setting where several more guild members may also be interaction, a single disruptive interaction may be mitigated by other intraguild interactions that are additive or synergistic.

Bibliography

Altieri, M. A. 1995. Agroecology: the science of sustainable agriculture. 2nd ed. Westview Press, Boulder, CO.

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Ag. Ecosyst. Environ. 74: 19-31.

Alvarez, J. M., R. Van Driesche and J. Cornell. 1999. Effect of *Encarsia* sp. nr. *diaspidicola* (Hymenoptera: Aphelinidae) parasitism on *Cybocephalus* sp. nr. *nipponicus* (Coleoptera: Cybocephalidae) egg laying choices. Biol. Control 15: 57-63.

Anderson, A. C. and K. V. Yeargan. 1998. Influence of soybean canopy closure on predator abundances and predation on *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs. Environ. Entomol. 27: 1488-1495.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Ann. Rev. Entomol. 36: 561-586.

Angalet, G. W., J. M. Tropp and A. N. Eggert. 1979. *Coccinella septempunctata* in the United States: recolonizations and notes on its ecology. Environ. Entomol. 8: 896-901.

Argov, Y. and Y. Rossler. 1998. Rearing methods for the citrus leafminer *Phyllocnistis citrella* Stainton and its parasitoids in Israel. Biol. Control 11: 18-21.

Ballal, C. R. and S. P. Singh. 1999. Host plant-mediated orientational and ovipositional behavior of three species of chrysopids (Neuroptera: Chrysopidae). Biol. Control 16: 47-57.

Banks, J. E. 1999. Differential response of two agroecosystem predators, *Pterostichus melanarius* (Coleoptera: Carabidae) and *Coccinella septempunctata* (Coleoptera: Coccinellidae), to habitat-composition and fragmentation-scale manipulations. Canad. Entomol. 131: 645-657.

Barbosa, P. [ed.] 1998. Conservation biological control. Academic Press, San Diego.

Barbosa, P. And S. D. Wratten. 1998. Influence of plants on invertebrate predators: implications to conservation biological control. In: P. Barbosa [ed.] Conservation biological control, pp. 83-100. Academic Press, San Diego.

Bellows, T. S. and R. G. Van Driesche. 1999. Life table construction and analysis for evaluating biological control agents. In: T. S. Bellows and T. W. Fisher [eds.] Handbook of Biological Control, pp. 199-223. Academic Press, San Diego.

Bellows, T. S., Jr., C. Meisenbacher and D. H. Headrick. 1998. Field biology of *Paraleyrodes minei* (Homoptera: Aleyrodidae) in southern California. Environ. Entomol. 27: 277-281.

Berberet, R. C. and A. D. Bisges. 1998. Potential for competition among natural enemies of larvae of *Hypera postica* (Coleoptera: Curculionidae) in the Southern Plains. Environ. Entomol. 27: 743-751.

Bigger, D. S. and W. E. Chaney. 1998. Effects of *Iberis umbellata* (Brassicaceae) on insect pests of cabbage and on potential biological control agents. Environ. Entomol. 27: 161-167.

Birch, L. C. 1957. The meanings of competition. Am. Nat. 16: 5-18.

Bottrell, D. G., P. Barbosa and F. Gould. 1998. Manipulating natural enemies by plant variety selection and modification: a realistic strategy? Ann. Rev. Entomol. 43: 347-367.

Boyd, M. L. and D. J. Boethel. 1998. Residual toxicity of selected insecticides to heteropteran predaceous species (Heteroptera: Lygaeidae, Nabidae, Pentatomidae) on soybean. Environ. Entomol. 27: 154-160.

Brewer, M. J., J. M. Struttmann and D. W. Mornhinweg. 1998. *Aphelinus albipodus* (Hymenoptera: Aphelinidae) and *Diaeretiella rapae* (Hymenoptera: Braconidae) parasitism on *Diuraphis noxia* (Homoptera: Aphididae) infesting barley plants differing in plant resistance to aphids. Biol. Control 11: 255-261.

Briggs, C. J. 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. Am. Nat. 141: 372-397.

Brownbridge, M., A. Adamowicz, M. Skinner and B. L. Parker. 1999. Prevalence of fungal entomopathogens in the life cycle of pear thrips, *Taeniothrips inconsequens* (Thysanoptera: Thripidae), in Vermont sugar maple forests. Biol. Control 16: 54-59.

Bruck, D. J. and L. C. Lewis. 1998. Influence of adjacent cornfield habitat, trap location, and trap height on capture numbers of predators and a parasitoid of the European corn borer (Lepidoptera: Pyralidae) in central Iowa. Environ. Entomol. 27: 1557-1562.

Campbell, R. E. 1926. The pea aphis in California. J. Ag. Res. 32: 861-881.

Carlson, D. A., C. J. Geden and U. R. Bernier. 1999. Identification of pupal exuviae of *Nasonia vitripennis* and *Muscidifurax raptorellus* parasitoids using cuticular hydrocarbons. Biol. Control 15: 97-106. Multiple predator species for biological control.

Chang, G. C. 1996. Comparison of single versus multiple species of generalist predators for biological control. Environ. Entomol. 25: 207-212.

Chang, G. C. 1998. *Chrysoperla plorabunda* (Neuroptera: Chrysopidae) larvae feed disproportionately on thrips (Thysanoptera: Thripidae) in the field. Canad. Entomol. 130: 549-550.

Chang, G. C. and P. Kareiva. 1999. The case for indigenous generalists in biological control. In: Theoretical approaches to biological control, B. A. Hawkins and H. V. Cornell [eds.], pp. 103-115. Cambridge University Press.

Chenot, A. B. and K. F. Raffa. 1998. Effects of parasitoid strain and host instar on the interaction of *Bacillus thuringiensis* subsp. *kurstaki* with the gypsy moth (Lepidoptera: Lymantriidae) larval parasitoid *Cotesia melanoscela* (Hymenoptera: Braconidae). Environ. Entomol. 27: 137-147.

Chilcutt, C. F. and B. E. Tabashnik. 1999. Simulation of integration of *Bacillus thuringiensis* and the parasitoid *Cotesia plutellae* (Hymenoptera: Braconidae) for control of susceptible and resistant diamondback moth (Lepidoptera: Plutellidae). Environ. Entomol. 28: 505: 512.

Cohen, J. E., K. Schoenly, K. L. Heong, H. Justo, G. Arida, A. T. Barrion and J. A. Litsinger. 1994. A food web approach to evaluating the effect of insecticide spraying on insect pest population dynamics in a Philippine irrigated rice ecosystem. J. Appl. Ecol. 31: 747-763.

Colunga-Garcia, M. and S. H. Gage. 1998. Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ. Entomol. 27: 1574-1580.

Crespo, D. C., R. E. Lecuona and J. A. Hogsette. 1998. Biological control: an important component in integrated management of *Musca domestica* (Diptera: Muscidae) in caged-layer poultry houses in Buenos Aires, Argentina. Biol. Control. 13: 16-24.

Crist, T. O. and R. G. Ahern. 1999. Effects of habitat patch size and temperature on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in an old field. Environ. Entomol. 28: 681-689.

Croft, B. A. and D. H. Slone. 1998. Perturbation of regulated apple mites: immigration and pesticide effects on outbreaks of *Panonychus ulmi* and associated mites (Acari: Tetranychidae, Eriophyidae, Phytoseiidae and Stigmaeidae). Environ. Entomol. 27: 1548-1556.

Croft, B. A., L. N. Monetti and P. D. Pratt. 1998. Comparative life histories and predation types: are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) similar type II selective predators of spider mites? Environ. Entomol. 27: 531-538.

Debach, P. 1946. An insecticidal check method for measuring the efficacy of entomophagous insects. J. Econ. Entomol. 39: 695-697.

Debach, P. 1974. Biological control by natural enemies. Cambridge University Press.

Debach, P. and B. Bartlett. 1951. Effects of insecticides on biological control of insect pests of citrus. J. Econ. Entomol. 44: 372-383.

Degooyer, T. A., L. P. Pedigo and M. E. Rice. 1999. Effect of alfalfa-grass intercrops on insect populations. Environ. Entomol. 28: 703-710.

De Moraes, R. R., J. E. Funderburk and J. E. Maruniak. 1998. Polymerase chain reaction techniques to detect multiple-nucleopolyhedrovirus in *Anticarsia gemmatalis* (Lepidoptera: Noctuidae) and predator populations in soybean. Environ. Entomol. 27: 968-975.

Digweed, S. C. 1998. Mortality of birch leafmining sawflies (Hymenoptera: Tenthredinidae): impacts of natural enemies on introduced pests. Environ. Entomol. 27: 1357-1367.

Dill, L. M.. A. H. G. Fraser and B. D. Roitberg. 1990. The economics of escape behaviour in the pea aphid, *Acyrthosiphon pisum*. 83: 473-478.

Dixon, A. F. G. 1958. Escape responses shown by certain aphids to the presence of the coccinellid, *Adalia decempunctata* (L.) Trans. R. Entomol. Soc. Lond. 10: 319-334.

Dry, F. E., D. C. Steinkraus and R. W. McNew. 1999. Microsporidia (Protozoa: Microspora) in pteromalids (Hymenoptera: Pteromalidae) in broiler-breeder houses of Northwest Arkansas. Biol. Control. 16: 164-169.

Dunn, J. A. and D. W. Wright. 1955. Population studies of the pea aphid in East Anglia. Bull. Entomol. Res. 46: 369-392.

Ehler, L. E. 1998. Conservation biological control: past, present, and future. In: P. Barbosa [ed.] Conservation biological control, pp. 1-8. Academic Press, San Diego.

Ehler, L. E. and J. C. Miller. 1978. Biological control in temporary agroecosystems. Entomophaga 23: 207-212.

Ehler, L. E. and R. W. Hall. 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. Environ. Entomol. 11: 1-4.

Ehler, L. E. and R. W. Hall. 1984. Evidence for competitive exclusion of introduced natural enemies in biological control: an addendum. Environ. Entomol. 13: v – vii.

Eigenbrode, S. D., C. White, M. Rohde and C. J. Simon. 1998. Behavior and effectiveness of adult *Hippodamia convergens* (Coleoptera: Coccinellidae) as a predator of *Acyrthosiphon pisum* (Homoptera: Aphididae) on a wax mutant of *Pisum sativum*. Environ. Entomol. 27: 902-909.

Elliot, N., R. Kieckhefer and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia 105: 537-544.

Evans, E. W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. Oecologia 87: 401-408.

Evans, E. W. and S. England. 1996. Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. Ecol. Appl. 6: 920-930.

Evans, H. F. 1976. The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum*. Ecol. Entomol. 1: 85-90.

Fagan, W. F. and L. E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75: 2022-2032.

Fagan, W. F., A. L. Hakim, H. Ariawan and S. Yuliyantiningsih. 1998. Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. Biol. Control 13: 121-126.

Feeny, P. 1976. Plant apparency and chemical defense. Recent Adv. Phytochem. 10: 1-40.

Ferguson, K. I. and P. Stiling. 1996. Non-additive effects of multiple natural enemies on aphid populations. Oecologia 108: 375-379.

Ferreira de Almeida, M. A. and A. Pires do Prado. 1999. *Aleochara* spp. (Coleoptera: Staphylinidae) and pupal parasitoids (Hymenoptera: Pteromalidae) attacking symbovine fly pupae (Diptera: Muscidae, Sarcophagidae and Otitidae) in southeastern Brazil. Biol. Control 14: 77-83.

Ferro, D. N. and J. N. McNeil. 1998. Habitat enhancement and conservation of natural enemies of insects. In: P. Barbosa [ed.] Conservation biological control, pp. 123-132. Academic Press, San Diego.

Fluke, C. L. 1929. The known predacious and parasitic enemies of the pea aphid in North America. Res. Bull. Wisc. Ag. Exp. Sta. #93: 1-47.

Force, D. C. 1974. Ecology of insect host-parasitoid communities. Science 184: 624-632.

Fox, L. R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. Syst. 6: 87-106

Frazer, B. D. 1977. Plant virus epidemiology and computer simulation of aphid populations. In: Aphids as virus vectors, K. F. Harris and K. Maramorosch [eds.] pp. 413-431. Academic Press, San Francisco.

French, B. W., N. C. Elliot and R. C. Berberet. 1998. Reverting conservation reserve program lands to wheat and livestock production: effects on ground beetle (Coleoptera: Carabidae) assemblages. Environ. Entomol. 27: 1323-1335.

French, B. W. and N. C. Elliot. 1999. Spatial and temporal distribution of ground beetle (Coleoptera: Carabidae) assemblages in riparian strips and adjacent wheat fields. Environ. Entomol. 28: 597-607.

Gaasch, C. M., J. Pickering and C. T. Moore. 1998. Flight phenology of parasitic wasps (Hymenoptera: Ichneumonidae) in Georgia's Piedmont. Environ. Entomol. 27: 606-614.

Geden, C. J. 1999. Host location by house fly (Diptera: Muscidae) parasitoids in poultry manure at different moisture levels and host densities. Environ. Entomol. 28: 755-760.

Geden, C. J., U. R. Bernier, D. A. Carlson and B. D. Sutton. 1998. Identification of *Muscidifurax* spp., parasitoids of muscoid flies, by composition patterns of cuticular hydrocarbons. Biol. Control. 12: 200-207.

Geervliet, J. B. F., S. Ariens, M. Dicke and L. E. M. Vet. 1998. Long-distance assessment of patch profitability through volatile infochemicals by the parasitoid *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae). Biol. Control. 11: 113-121.

Gerling, D. and S. E. Naranjo. 1998. The effect of insecticide treatments in cotton fields on the levels of parasitism of *Bemisia tabaci* (Gennadius) sl. Biol. Control. 12: 33-41.

Gerritsen, L. J. M., G. L. Wiegers and P. H. Smits. 1998. Pathogenicity of new combinations of *Heterorhabditis* spp. and *Photorhabdus luminescens* against *Galleria mellonella* and *Tipula oleracea*. Biol. Control. 13: 9-15.

Gonzalez-Hernandez, H., M. W. Johnson and N. J. Reimer. 1999. Impact of *Pheidole megacephala* (F.) (Hyenoptera: Formicidae) on the biological control of *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae). Biol. Control 15: 145-152.

Goolsby, J. A., M. A. Ciomperlik, B. C. Legaspi, Jr., J. C. Legaspi and L. E. Wendel. 1998. Laboratory and field evaluation of exotic parasitoids of *Bemisia tabaci* (Gennadius) (Biotype "B") (Homoptera: Aleyrodidae) in the Lower Rio Grande Valley of Texas. Biol. Control. 12: 127-135.

Grafton-Cardwell, E. E., Y. Ouyang, and R. A. Striggow. 1999. Predacious mites for control of citrus thrips, *Scirtothrips citri* (Thysanoptera: Thripidae) in nursery citrus. Biol. Control 14: 29-36.

Greenberg, S. M., D. A. Nordlund and Z. Wu. 1998. Influence of rearing host on adult size and ovipositional behavior of mass produced female *Trichogramma minutum* Riley and *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae). Biol. Control. 11: 43-48.

Grevstad, F. S. and B. W. Klepetka. 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. Oecologia 92: 399-404.

Grushecky, S. T., A. M. Liebhold, R. Greer and R. L. Smith. 1998. Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantriidae) larvae and pupae? Environ. Entomol. 27: 268-276.

Gutierrez, A. P. 1992. Physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm. Ecology 73: 1552-1563.

Gutierrez, A. P., J. U. Baumgaertner and C. G. Summers. 1984. Multitrophic models of predator-prey energetics. Canad. Entomol. 116: 923-963.

Gutierrez, A. P., K. S. Hagen and C. K. Ellis. 1990. Evaluating the impact of natural enemies: a multitrophic perspective. In: Critical issues in biological control, M. Mackauer, L. E. Ehler and J. Roland [eds.], pp. 81-109. Intercept, Andover, UK.

Gutierrez, A. P., L. E. Caltagirone and W. Meikle. 1999. Evaluation of results. In: T. S. Bellows and T. W. Fisher [eds.] Handbook of Biological Control, pp. 243-252. Academic Press, San Diego.

Hassan, S. A., F. Klinghauf and F. Shahin. 1985. Role of *Chrysopa carnea* as an aphid predator on sugar beet and the effect of pesticides. Z. Ange. Entomol. 100: 163-174.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press.

Hatting, J. L., R. A. Humber, T. J. Poprawski and R. M. Miller. 1999. A survey of fungal pathogens of aphids from South Africa, with special reference to cereal aphids. Biol. Control 16: 1-12.

Hawkins, B. A., H. V. Cornell and M. E. Hochberg. 1997. Predators, parasitoids, ad pathogens as mortality agents in phytophagous insect populations. Ecology 78: 2145-2152.

Heimpel, G. E., J. A. Rosenheim and M. Mangel. 1997. Predation on adult *Aphytis* parasitoids in the field. Oecologia 110: 346-352.

Heinz, K. M. and M. P. Parrella. 1998. Host location and utillization by selected parasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae): implications for augmentative biological control. Environ. Entomol. 27: 773-784.

Heinz, K. M. 1998. Dispersal and dispersion of aphids (Homoptera: Aphididae) and selected natural enemies in spatially subdivided greenhouse environments. Environ. Entomol. 27: 1029-1038.

Herard, F. and G. Mercadier. 1996. Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col., Scolytidae) on *Pinus sylvestris* near Orleans, France: temporal occurrence and relative abundance, and notes on eight predatory species. Entomophaga 41: 183- 210.

Hodge, M. A. 1999. The implications of intraguild predation for the role of spiders in biological control. J. Arachnology 27: 351-362.

Hodgson, P. J., J. Sivinski, G. Quintero and M. Aluja. 1998. Depth of pupation and survival of fruit fly (*Anastrepha* spp.: Tephritidae) pupae in a range of agricultural habitats. Environ. Entomol. 27: 1310-1314.

Hölldobler, B. and E. O. Wilson. 1990. The ants. Harvard University Press.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canad. Entomol. 91: 293-320.

Horgan, F. G., J. H. Myers and R. Van Meel. 1999. Cyzenis albicans (Diptera: Tachinidae) does not prevent the outbreak of winter moth (Lepidoptera: Geometridae) in birch stands and blueberry plots on the lower mainland of British Columbia. Environ. Entomol. 28: 96-107.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100: 419-424.

Hostetler, M. 1997. That gunk on your car. Ten Speed Press, Berkeley, CA.

Howarth, F. G. 1991. Environmental impacts of classical biological control. Ann. Rev. Entomol. 36: 485-509.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343-383.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287: 308-309.

Hunter, M. D., G. C. Varley and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. Proc. Natl. Acad. Sci. 94: 9176-9181.

Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. Ecol. Monogr. 61: 75-94.

James, R. R., B. A. Croft, B. T. Shaffer and B. Lighthart. 1998. Impact of temperature and humidity on host-pathogen interactions between *Beauveria bassiana* and a coccinellid. Environ. Entomol. 27: 1506-1513.

James, D. G., M. M. Stevens, K. J. O'Malley and R. J. Faulder. 1999. Ant foraging reduces the abundance of beneficial and incidental arthropods in citrus canopies. Biol. Control 14: 121-126.

Jewett, D. K. and J. E. Carpenter. 1999. Chemically-mediated attraction of *Ichneumon* (= *Pterocormus*) *promissorius* (Hymenoptera: Ichneumonidae) males by females. Environ. Entomol. 28: 551-556.

Jones, W. A., M. A. Ciomperlik and D. A. Wolfenbarger. 1998. Lethal and sublethal effects of insecticides on two parasitoids attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae). Biol. Control 11: 70-76.

Kareiva, P. 1990. The spatial dimension in pest-enemy interactions. In: Critical issues in biological control, M. Mackauer, L. E. Ehler and J. Roland [eds.], pp. 213-227. Intercept, Andover, UK.

Kareiva, P. and R. Sahakian. 1990. Tritrophic effects of a simple architectural mutation in pea plants. Nature 345: 433-434.

Keller, M. A. 1984. Reassessing evidence for competitive exclusion of introduced natural enemies. Environ. Entomol. 13: 192-195.

Kester, K. M. and D. M. Jackson. 1996. When good bugs go bad: intraguild predation by *Jalysus wickhami* on the parasitoid, *Cotesia congregata*. Entomol. Exp. Appl. 81: 271-276.

Kindlmann, P. and Z. Ruzicka. 1992. Possible consequences of a specific interaction between predators and parasites of aphids. Ecol. Modelling 61: 253-265.

Koppenhofer, A. M., H. Y. Choo, H. K. Kaya, D. W. Lee and W. D. Gelernter. 1999. Increased field and greenhouse efficacy against scarab grubs with a combination of an entomopathogenic nematode and *Bacillus thuringiensis*. Biol. Control 14: 37-44.

Kyei-Poku, G. K. and Y. Kunimi. 1998. Nondevelopment of *Cotesia kariyai* (Hymenoptera: Braconidae) in entomopoxvirus-infected larvae of *Pseudaletia separata* (Lepidoptera: Noctuidae). Biol. Control 11: 209-216.

Lacey, L. A. and T. R. Unruh. 1998. Entomopathogenic nematodes for control of codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae): effect of nematode species, concentration, temperature, and humidity. Biol. Control 13: 190-197.

Lam, W.-K. F. and L. P. Pedigo. 1998. Response of soybean insect communities to row width under crop-residue management systems. Environ. Entomol. 27: 1069-1079.

Landis, D. A. and F. D. Menalled. 1998. Ecological considerations in the conservation of effective parasitoid communities in agricultural systems. In: P. Barbosa [ed.] Conservation biological control, pp. 101-121. Academic Press, San Diego.

Lewis, W. J., J. C. van Lenteren, S. C. Phatak and J. H. Tumlinson III. 1997. A total system approach to sustainable pest management. Proc. Natl. Acad. Sci. USA 94: 12243-12248.

Liebhold, A. M., Y. Higashiura and A. Unno. 1998. Forest type affects predation on gypsy moth (Lepidoptera: Lymantriidae) pupae in Japan. Environ. Entomol. 27: 858-862.

Lockwood, J. A. 1993. Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. Environ. Entomol. 22: 503-518.

Lopez, M., M. Aluja and J. Sivinski. 1999. Hymenopterous larval-pupal and pupal parasitoids of *Anastrepha* flies (Diptera: Tephritidae) in Mexico. Biol. Control 15: 119-129.

Losey, J. E. and R. F. Denno. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79: 2143-2152.

Losey, J. E. and R. F. Denno. 1999. Factors facilitating synergistic predation: the central role of synchrony. Ecol. Appl. 9: 378-386.

Lucas, E., D. Coderre and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. Ecology. 79: 1084-1092.

Lucas, E. and J. Brodeur. 1999. Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). Environ. Entomol. 28: 622-627.

Luck, R. F., B. M. Shepard and P. E. Kenmore. 1999. Evaluation of biological control with experimental methods. In: T. S. Bellows and T. W. Fisher [eds.] Handbook of Biological Control, pp. 225-242. Academic Press, San Diego.

Malakar, R., J. S. Elkinton, S. D. Carroll and V. D'Amico. 1999. Interactions between two gypsy moth (Lepidoptera: Lymantriidae) pathogens: nucleopolyhedrovirus and *Entomophaga maimaiga* (Zygomycetes: Entomophthorales): field studies and a simulation model. Biol. Control 16: 189-198.

Marks, R. J. 1977. Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. Bull. Entomol. Res. 67: 235-241.

Martinez Pico, M., C. Maldonado and R. Levins. 1965. Ecology and genetics of Puerto Rican Drosophila: I. Food preferences of sympatric species. Carib. J. Sci. 5: 29-37.

McCaffrey, J. P. and R. L. Horsburgh. 1982. Interspecific interactions between *Orius insidiosus* (Heteroptera: Anthocoridae) and *Leptothrips mali* (Thysanoptera: Phlaeothripidae). Environ. Entomol. 11: 1104-1107.

McCravy, K. W. and C. W. Berisford. 1998. Parasitism by *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) in relation to Nantucket pine tip moth (Lepidoptera: Tortricidae) egg density and location. Environ. Entomol. 27: 355-359.

McGregor, R., T. Hueppelsheuser, A. Luczynski and D. Henderson. 1998. Collection and evaluation of *Trichogramma* species (Hymenoptera: Trichogrammatidae) as biological controls of the oblique-banded leafroller *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae) in raspberries and blueberries. Biol. Control. 11: 38-42.

McKelvey, J. J. Jr. 1972. Pest control in health and agriculture: international challenges. In: Pest control strategies for the future, Agricultural Board, Division of Biology and Agriculture, National Research Council, pp. 7-17. National Academy of Sciences, Washington, D.C.

Meagher, R. L., Jr., J. W. Smith, Jr., H. W. Browning and R. R. Saldana. 1998. Sugarcane stemborers and their parasites in southern Texas. Environ. Entomol. 27: 759-766.

Mendel, Z., F. Assael, S. Zeidan and A. Zehavi. 1998. Classical biological control of *Palaeococcus fuscipennis* (Burmeister) (Homoptera: Margarodidae) in Israel. Biol. Control. 12: 151-157.

Metcalf, R. L. and R. A. Metcalf. 1993. Destructive and useful insects: Their habits and control. McGraw-Hill, New York.

Morrill, W. L., G. D. Kushnak and J. W. Gabor. 1998. Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) in Montana. Biol. Control. 12: 159-163.

Murdoch, W. W., J. D. Reeve, C. B. Huffaker and C. E. Kennett. 1984. Biological control of olive scale and its relevance to ecological theory. Am. Nat. 123: 371-392.

Myers, J. H., C. Higgins and E. Kovacs. 1989. How many insect species are necessary for the biological control of insects? Environ. Entomol. 18: 541-547.

Nabli, H., W. C. Bailey and S. Necibi. 1999. Beneficial insect attraction to light traps with different wavelengths. Biol. Control. 16: 185-188.

Nafus, D. M. 1993. Movement of introduced biological control agents onto nontarget butterflies, *Hypolimnas* spp. (Lepidoptera: Nymphalidae). Environ. Entomol. 22: 265-272.

Nakai, M. and Y. Kunimi. 1998. Effects of the timing of entomopoxvirus administration to the smaller tea tortrix, *Adoxophyes* sp. (Lepidoptera: Tortricidae) on the survival of the endoparasitoid, *Ascogaster reticulatus* (Hymenoptera: Braconidae). Biol. Control. 13: 63-69.

National Agricultural Statistics Service. 1997. Agricultural Chemical Usage Vegetables 1996 Summary. USDA, Washington D.C.

National Commission on Small Farms. 1998. A time to act. USDA, Washington D.C.

Obrycki, J. J., K. L. Giles and A. M. Ormond. 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. Oecologia 117: 279-285.

Ogol, C. K. P. O., J. R. Spence and A. Keddie. 1998. Natural enemy abundance and activity in a maize-leucana agroforestry system in Kenya. Environ. Entomol. 27: 1444-1451.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355: 73-75.

Parry, D., J. R. Spence and W. J. A. Volney. 1998. Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocompidae). Envion. Entomol. 27: 1368-1374.

Pell, J.K., R. Pluke, S. J. Clark, M. G. Kenward, and P. G. Alderson. 1997. Interactions between two aphid natural enemies, the entomopathogenic fungus *Erynia neoaphidis* Remaudiere & Hennebert (Zygomycetes: Entomophthorales) and the Predatory Beetle *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). J. Invert. Pathol. 69: 261-268.

Peng, R. K., L. D. Incoll, S. L. Sutton, C. Wright and A. Chadwick. 1993. Diversity of airborne arthropods in a silvoarable agroforestry system. J. Appl. Ecol. 30: 551-562.

Perfecto, I. and A. Castineiras. 1998. Deployment of the predaceous ants and their conservation in agroecosystems. In: P. Barbosa [ed.] Conservation Biological Control, pp. 269-289. Academic Press, San Diego.

Pfannenstiel, R. S. and K. V. Yeargan. 1998. Association of predaceous Hemiptera with selected crops. Environ. Entomol. 27: 232-239.

Polis, G. A. and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. 7: 151-154.

Polis, G. A., C. A. Myers and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. Syst. 20: 297-330.

Poprawski, T. J., J. C. Legaspi and P. E. Parker. 1998. Influence of entomopathogenic fungi on *Serangium parcesetosum* (Coleoptera: Coccinellidae), an important predator of whiteflies (Homoptera: Aleyrodidae). Environ. Entomol. 27: 785-795.

Prasifka, J. R., P. C. Krauter, K. M. Heinz, C. G. Sansone and R. R. Minzenmayer. 1999. Predator conservation in cotton: using grain sorghum as a source for insect predators. Biol. Control. 223-229.

Readio, J. and M. H. Sweet. 1982. A review of the Geocorinae of the United States east of the 100th meridian (Hemiptera: Lygaeidae). Misc. Pub. Entomol. Soc. Am. 12: 1-91.

Rice, M. E. 1992. High altitude occurrence and westward expansion of the seven-spotted lady beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in the Rocky Mountains. Coleopt. Bull. 46: 142-143.

Ridgway, R. L. and S. L. Jones. 1968. Field-cage releases of *Chrysopa carnea* for suppression of populations of the bollworm and the tobacco budworm on cotton. J. Econ. Entomol. 61: 892-898.

Ridgway, R. L. and S. L. Jones. 1969. Inundative releases of *Chrysopa carnea* for control of *Heliothis* on cotton. J. Econ. Entomol. 62: 177-180.

Riechert, S. E., L. Provencher and K. Lawrence. 1999. The potential of spiders to exhibit stable equilibrium point control of prey: tests of two criteria. Ecol. Appl. 9: 365-377.

Riudavets, J. and C. Castane. 1998. Identification and evaluation of native predators of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in the Mediterranean. Environ. Entomol. 27: 86-93.

Roitberg, B. D. and J. H. Myers. 1979. Behavioural and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbance. Canad. Entomol. 111: 515-519.

Roitberg, B. D., J. H. Myers and B. D. Frazer. 1979. The influence of predators on the movement of apterous pea aphids between plants. J. Anim. Ecol. 48: 111-122.

Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37: 317-350.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol. Monogr. 43: 95-124.

Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Ann. Rev. Entomol. 43: 421–47.

Rosenheim, J. A, D. D. Limburg and R. G. Colfer. 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. Ecol. Appl. 9: 409-417.

Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biol. Control 5: 303-335.

Rosenheim, J. A., L. R. Wilhoit and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96: 439-449.

Rossi, L. 1999. Methyl parathion, receipt of requests for cancellation; cancellation order. Federal Register 64: 57877-57881.

Rothwell, N. L. and D. R. Smitley. 1999. Impact of golf course mowing practices on *Ataenius spretulus* (Coleoptera: Scarabaeidae) and its natural enemies. Environ. Entomol. 28: 358-366.

Roy, H.E., J. K. Pell, S. J. Clark, and P. G. Alderson. 1998. Implications of predator foraging on aphid pathogen dynamics. J. Invert. Pathol. 71: 236-247.

Roy, M., J. Brodeur and C. Cloutier. 1999. Seasonal abundance of spider mites and their predators on red raspberry in Quebec, Canada. Environ. Entomol. 28: 735-747.

Rutledge, C. E. and R. N. Wiedenmann. 1999. Habitat preferences of three congeneric braconid parasitoids: implications for host-range testing in biological control. Biol. Control. 16: 144-154.

Ruzicka, Z. 1976. Prey selection by larvae of Metasyrphus corollae (Diptera, Syrphidae). Acta Entomol. Bohemoslov. 73: 305-311.

Sands, D. P. A. and M. T. Coombs. 1999. Evaluation of the Argentinian parasitoid Trichopoda giacomellii (Diptera: Tachinidae), for biological control of Nezara viridula (Hemiptera: Pentatomidae) in Australia. Biol. Control. 15: 19-24.

Schaefer, P. W., R. J. Dysart and H. B. Specht. North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. Environ. Entomol. 16: 368-373.

Schausberger, P. and B. A. Croft. 1999a. Activity, feeding, and development among larvae of specialist and generalist phytoseiid mite species (Acari: Phytoseiidae). Environ. Entomol. 28: 322-329.

Schausberger, P. and B. A. Croft. 1999b. Predation on and discrimination between con- and heterospecific eggs and specialist and generalist phytoseiid mites (Acari: Phytoseiidae). Environ. Entomol. 28: 523-528.

Schellhorn, N. A. and D. A. Andow. 1999a. Cannibalism and interspecific predation: role of oviposition behavior. Ecol. Appl. 9: 418-428.

Schellhorn, N. A. and D. A. Andow. 1999b. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. Environ. Entomol. 28: 1092-1100.

Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Schoener, T. W. 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. Theor. Pop. Biol. 10: 309-333.

Schoenly, K. G., H. D. Justo, Jr., A. T. Barrion, M. K. Harris and D. G. Bottrell. 1998. Analysis of invertebrate biodiversity in a Philippine farmer's irrigated rice field. Environ. Entomol. 27: 1125-1136.

Schreiber, S. J. and A. P. Gutierrez. 1998. A supply/demand perspective of species invasions and coexistence: applications to biological control. Ecol. Modelling 106: 27-45.

Schroeder, L. M. 1996. Interactions between the predators *Thanasimus formicarius* (Col.: Cleridae) and *Rhizophagus depressus* (Col.: Scolytidae). Entomophaga 41: 63-75.

Schultz, C. B. and G. C. Chang. 1998. Challenges in insect conservation: managing fluctating populations in disturbed habitats. In: *Conservation Biology: for the coming decade*, 2nd ed. P. L. Fiedler and P. M. Kareiva, eds, pp. 228-254. Chapman & Hall, San Francisco.

Scopes, N. E. A. 1969. The potential of *Chrysopa carnea* as a biological control agent of *Myzus persicae* on glasshouse chrysanthemums. Ann. Appl. Biol. 64: 433-439.

Secord, D. and P. Kareiva. 1996. Perils and pitfalls in the host specificity paradigm. BioScience 46: 448-453.

Sengonca, C. and B. Frings. 1985. Interference and competitive behavior of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata* in the laboratory. Entomophaga 30: 245-251.

Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, Pajarningsih and Sartanto. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77: 1975-1988.

Severance, G. 1911. Field peas on a Palouse wheat farm. Washington Ag. Exp. Sta. Popular Bull. No. 36.

Sih, A., G. Englund and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13: 350-355.

Silva, I. M. M. S., J. Honda, F. van Kan, J. Hu, L. Neto, B. Pintureau and R. Stouthamer. 1999. Molecular differentiation of five *Trichogramma* species occurring in Portugal. Biol. Control. 16: 177-184.

Sivinski, J., K. Vulinec, E. Menezes and M. Aluja. 1999. The bionomics of Coptera haywardi (Oglobin) (Hymenoptera: Diapriidae) and other pupal parasitoids of tephritid fruit flies (Diptera). Biol. Control. 11: 193-202.

Slone, D. H. and B. A. Croft. 1998. Spatial aggreagtion of apple mites (Acari: Phytoseiidae, Stigmaeidae, Tetranychidae) as measured by a binomial model: effects of lofe stage, reproduction, competition, and predation. Environ. Entomol. 27: 918-925.

Smitley, D. R., T. W. Davis and N. L. Rothwell. 1998. Spatial distribution of *Ataenius spretulus*, *Aphodius granarius* (Coleoptera: Scarabaeidae), and predaceous insects across golf course fairways and roughs. Environ. Entomol. 27: 1336-1349.

Snyder, W. E. and D. H. Wise. 1999. Predator interference and the establishment of generalist predator populations for biocontrol. Biol. Control 15: 283-292.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd ed. Freeman, New York.

Speight, M. R. 1983. The potential of ecosystem management for pest control. Ag. Ecosyst. Environ. 10: 183-199.

Stark, D. M., N. J. Mills and A. H. Purcell. 1999. Interactions between the parasitoid *Ametadoria misella* (Diptera: Tachinidae) and the granulovirus of *Harrisina brillians* (Lepidoptera: Zygaenidae). Biol. Control. 14: 146-151.

Strong, D. R. and R. W. Pemberton. 2000. Biological control of invading species--risk and reform. Science 288: 1969-1970.

Suenaga, H. and T. Hamamura 1998. Laboratory evaluation of carabid beetles (Coleoptera: Carabidae) as predators of diamondback moth (Lepidoptera: Plutellidae) larvae. Environ. Entomol. 27: 767-772.

Sweetman, H. L. 1936. The biological control of insects. Comstock, Ithaca, NY.

SYSTAT. 1997. SYSTAT for Windows, version 7.0.1. SPSS Inc., Chicago, IL.

Takagi, M. and Y. Hirose. 1994. Building parasitoid communities: the complementary role of two introduced parasitoid species in a case of successful biological control. In: Parasitoid community ecology, B. A. Hawkins and W. Sheehan [eds.], pp. 437-448. Oxford University Press, New York.

Tauber, M. J., C. A. Tauber, K. M. Daane and K. S. Hagen. 2000. Commercialization of predators: recent lessens from green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). Am. Entomol. 46: 26-38.

Taylor, D. B. and A. L. Szalanski. 1999. Identification of *Muscidifurax* spp. by polymerase chain reaction–restriction fragment length polymorphism. Biol. Control 15: 270-273.

Taylor, D. B., A. L. Szalanski, B. J. Adams and R. D. Peterson II. 1998. Susceptibility of house fly (Diptera: Muscidae) larvae to entomopathogenic nematodes (Rhabditida: Heterorhabditidae, Steinernematidae). Environ. Entomol. 27: 1514-1519.

Tipping, P. W., C. A. Holko, A. A. Abdul-Baki and J. R. Aldrich. 1999. Evaluating *Edovum puttleri* Grissell and *Podisus maculiventris* (Say) for augmentative biological control of Colorado potato beetle in tomatoes. Biol. Control 16: 35-42.

Tisdell, C. A. 1990. Economic impact of biological control of weeds and insects. In: Critical issues in biological control, M. Mackauer, L. E. Ehler and J. Roland [eds.], pp. 301-316. Intercept, Andover, UK.

USA Dry Pea & Lentil Council. 1999. U. S. pea, lentil and chickpea seeded acreage report. Moscow, ID.

U.S. Congress, Office of Technology Assessment. 1995. Biologically based technologies for pest control, OTA-ENV-636. Washington, D.C.: U.S. Government Printing Office.

Valladares, G. R. and A. Salvo. 1999. Insect-plant food webs could provide new clues for pest management. Environ. Entomol. 28: 539-543.

Waage, J. 1990. Ecological theory and the selection of biological control agents. In: Critical issues in biological control, M. Mackauer, L. E. Ehler and J. Roland [eds.], pp. 135-157. Intercept, Andover, UK.

Wardle, R. A. and P. Buckle. 1923. The principles of insect control. University of Manchester Press, New York.

Wei, H., R. A. Goyer and G. Lenhard. 1998. Abundance of parasitoids of *Archips argyrospila* (Lepidoptera: Tortricidae) in Louisiana. Environ. Entomol. 27: 726-730.

Wells, M. L. and R. M. McPherson. 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). Environ. Entomol. 28: 768-773.

Weseloh, R. M. 1998. Modeling the influence of forest characteristics and ant (Formicidae: Hymenoptera) predation on dispersal and survival of neonate gypsy moths (Lymantriidae: Lepidoptera). Environ. Entomol. 27: 288-296.

Wilbur, H. M. and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. Am. Nat. 135: 176-204.

Wilson-Rummenie, A. C., B. J. Radford, L. N. Robertson, G. B. Simpson and K. L. Bell. 1999. Reduced tillage increases population density of soil macrofauna in a semiarid environment in central Queensland. Environ. Entomol. 28: 163-172.

Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biol. Control 10: 4-15.

Wunderlich, L. R. and D. K. Giles. 1999. Field assessment of adhesion and hatch of *Chrysoperla* eggs mechanically applied in liquid carriers. Biol. Control 14: 159-167.

Yencho, G. C., L. W. Getzin and G. E. Long. 1986. Economic injury level, action threshold, and a yield-loss model for the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae), on green peas, *Pisum sativum*. J. Econ. Entomol. 79: 1681-1687.

Ylioja, T., H. Roininen, M. P. Ayres, M. Rousi and P. W. Price. 1999. Host-driven population dynamics in an herbivorous insect. Proc. Natl. Acad. Sci. 96: 10735-10740.

Appendix A. Table of selected studies explicitly conducted to assess using multiple species together for biocontrol. Studies are listed alphabetically by citation. Column headings: **A**: Citation. **B**: Number of natural enemies in the study. **C**: Main pest species. **D**: Did the study use experimental (E) or strictly observational (O) methods? **E**: If experimental, did it incorporate a factorial design? ("+" denotes treatments in addition to the baseline two-factor experiment.) **F**: Tactical recommendation (if any). **G**: Mechanism underlying the recommendation (if known). **H**: Notes.

A	B	C	D	E	F	G	H
Chang 1996	2	*Aphis fabae*	E	yes +	no evidence against using *C. plorabunda* and *C. septempuncatata* together	habitat partitioning – different preferences for foraging locations	
Cohen et al. 1994	≥17	7 species	E	no	not explicit, but suggest considering multiple natural enemies for forecasting pest abundance	natural enemy interaction not addressed	
Elliott et al. 1996	8	unspecified aphids	O	no	suggests that the introduction of *C. septempunctata* has not improved pest management	introduction of *C. septempunctata* correlated w/ decrease in *C. transversoguttata* & *Adalia bipunctata*	
Evans 1991	4	*Acyrthosiphon pisum*	E	yes +	species diversity per se did not influence pest suppression	interspecific competition equalled intraspecific competition	

Evans & England 1996	2	*Hypera postica*	E	yes	raises concerns about the introduction of *C. septempunctata*	indirect effect: *C. septempunctata* reduced aphids, reducing honeydew for the other biocontrol agent	
Heimpel et al. 1997	≥6	*Quadraspidiotus perniciosus*	O	no	not explicit, but disruption is hinted	IGP by generalist on parasitoids	
Herard & Mercadier 1996	45	*Tomicus piniperda* & *Ips acuminatus*	O	no	multiple species promoted as useful biocontrol agents	temporal occurence suggests complementary interactions within guild	31 predators and 14 parasitoids
Kindlmann & Ruzicka 1992	2	*Brevicoryne brassicae* & *Myzus persicae*	E	no	syrphid added to parasitoid improves pest suppression; model predicts time-sensitivity	slight IGP on parasitized aphids, but syrphids much prefer unparasitized aphids	
Losey & Denno 1998	3	*Acyrthosiphon pisum*	E	yes	foliar-foraging and ground-foraging predators should both be present in alfalfa	defensive behavior of prey leads to increased predation risk, resulting in synergism	
Losey & Denno 1999	6	*Acyrthosiphon pisum*	O	no	synergism (in Losey & Denno 1998) suggests combining species	spatial partitioning mitigates IGP, temporal overlap in activity allows synergism	
Lucas et al. 1998	3	*Macrosiphum euphorbiae*	E	no	avoid releasing stages that are especially susceptible or especially prone to IGP	certain life stages of predators are more vulnerable to IGP; other stages are more prone to IGP	

McCaffrey & Horsburgh 1982	2	*Panonychus ulmi*	E	no	*O. insidiosus* & *L. mali* appear compatible	mutual avoidance the most frequent outcome of encounters, particularly with satiated *Orius*	
Obrycki et al. 1998	2	*Acyrthosiphon pisum*	E	yes +	*C. septempunctata* affects *Coleomegilla maculata* but not the prey	uncertain: exploitative competition and/or IGP	
Pell et al. 1997	2	*Acyrthosiphon pisum*	E	no	use of *C. septempunctata* and *E. neoaphidis* encouraged	some IGP occurs, but often incomplete, and predator can vector pathogen	pest population results unclear
Riechert et al. 1999	58	Orthoptera	E	yes	conserve the natural predatory assemblage	temporal dissimilarity in abundance of different spider species	old field (model) system
Rosenheim et al. 1993	7	*Aphis gossypii*	E	yes	disruption	IGP of hemipterans on *C. carnea*, interference also possible	
Rosenheim et al. 1999	6	*Aphis gossypii*	O	no	disruption (in Rosenheim et al. 1993) suggests situations where biocontrol is less likely to succeed	IGP	
Roy et al. 1998	5	*Acyrthosiphon pisum*	E	no	use of *C. septempunctata* and *E. neoaphidis* encouraged	vectoring of pathogen by predator outweighs IGP	additive or synergistic effect inferred
Schellhorn & Andow 1999	2	*Rhopalosiphum maidis*, other aphids	E	no	predict both species of predator will give better control than either alone	strength of cannibalism is greater than interspecific predation	intra- and inter-specific interactions compared

Schroeder 1996	2	*Tomicus piniperda*	E	yes	subadditive effect, but high mortality from predators renders additive model inappropriate	mortality from both = -89%, *Thanasimus* = -81%, *Rhizophagus* = -41%	
Settle et al. 1996	493	*Nilaparvata lugens* and others	E	no	practices should foster the early season abundance of a diverse set of predators	natural enemy interaction not addressed	306 predator and 187 parasitoid spp.

Appendix B. Table of studies published between January 1998 and October 1999 in *Environmental Entomology* and *Biological Control* that involve multiple biological control agents. Column headings: A: Citation. B: Number of natural enemies in the study. C: Main pest species. D: Did the study use experimental (E) or strictly observational (O) methods? E: If experimental, did it incorporate a factorial design? ("+" denotes treatments in addition to the baseline two-factor experiment.) F: Tactical recommendation (if any). G: Mechanism underlying the recommendation (if known). H: Notes.

Studies explicitly conducted to assess using multiple species of biocontrol agents together

A	B	C	D	E	F	G	H
Alvarez et al. 1999	2	*Unaspis euonymi*	E	no	use of both biocontrol agents appears unhindered by competition	beetles avoid ovipositing on parasitized scales	
Berberet & Bisges 1998	3	*Hypera postica*	O	no	none explicit	IGP – *Zoophyhora phytonomi* attacks *Bathyplectes curculionis*	
Chenot & Raffa 1998	2	*Lymantria dispar*	E	no	correct timing of Bt application may improve combined performance	variable responses of parasitoid to Bt	
Chilcutt & Tabashnik 1999	2	*Plutella xylostella*	*	no	use of parasitoids may slow evolution of pesticide resistance	unclear; results hold for both "IGP" and "partitioning" models	* simulation model
Colunga-Garcia & Gage 1998	12	unspecified	E	no	caution: the introduction of *Harmonia axyridis* has been correlated with declines in certain other coccinellids	unknown	unclear if total coccinellid density

							has changed
Crist & Ahern 1999	3	none specified	E	no	none	each natural enemy was most widespread and abundant in a different habitat	
Croft & Slone 1998	3	5 mite spp.	E	no	not explicit (not clear whether decrease in predator diversity or numbers is more important)	unknown	
Croft et al. 1998	2	*Tetranychus urticae*	E	no	none	slightly more inter- than intraspecific predation	
Digweed 1998	≥45	3 species of introduced sawflies	E	no	incumbent natural enemy guild lacks specialists that could provide better control	not addressed	18 parasitoids and at least 27 potential predators
Fagan et al. 1998.	≥2	delphacids & cicadellids	E	not w/ spp.	adding spiders improves pest control, but spiders & insecticide does not	IGP on mesoveliids combines additively with nontarget insecticide mortality	
Ferreira de Almeida & Pires do Prado. 1999	8	*Musca domestica* & *Stomoxys calcitrans*	O	no	multiple species promoted as useful biocontrol agents	habitat partitioning: prey location at different depths of manure, humidity	includes interspecific association index
French & Elliot 1999	101	*Schizaphis graminum*	O	no	multiple species promoted as candidate biocontrol agents	assemblages of carabids differ with respect to seasons	
Geden 1999	5	*Musca*	E	no	multiple parasitoid spp.	habitat partitioning - different	

		domestica			recommended for house fly control in poultry houses	humidity preferences	
Gerritsen et al. 1998	3	*Galleria mellonella* & *Tipula oleracea*	E	no	nematode and bacteria are symbionts and exhibit synergism at the level of individual prey	bacteria kills host while nematode disables host's immune system	
Grushecky et al. 1998	≥15	*Lymantria dispar*	E	no	ambivalent; increased predator abundance did not increase rates of predation	not clear	
Hodgson et al. 1998	≥20	*Anastrepha* spp.	E	no	suggest a hypothetical orchard management scheme using chickens and insect predators	habitat partitioning - chickens consume pupae on the soil surface, insect attack buried pupae	
James et al. 1998	2	*Acyrthosiphon pisum*	E	no	most IGP likely at low temperatures	increased susceptibility of *Hippodamia convergens* to *Beauveria bassiana* at lower temperatures	
Koppenhofer et al. 1999	3	scarab grubs (3 spp.)	E	yes	combination recommended for potential to control	unclear	
Kyei-Poku & Kunimi 1998	2	*Pseudaletia separata*	E	yes	not explicit, but within individual hosts parasitoid and pathogen antagonists	parasitoid fails to develop in virus-infected hosts	
Lacey & Unruh 1998	3	*Cydia pomonella*	E	no	not directly from experimental results, but suggest combining nematodes and virus	nematodes and granulosis virus attack different life stages of pest	
Lam & Pedigo 1998	≥7	*Empoasca fabae*	E	no	none, but lacewing population may be low due to IGP	*Orius insidiosus* suspected of feeding on lacewing eggs	

Lucas & Brodeur 1999	2	*Macrosiphum euphorbiae*	E	no	no tactical recommendation found	IGP occurs, but *Aphidoletes aphidimyza* reproduction is cheap	
Malakar et al. 1999	2	*Lymantria dispar*	E	no	in simulations, combined mortality always higher than nucleopolyhedralvirus alone	diseases attack different life stages of the pest	
Mendel et al. 1998	9	*Palaeococcus fuscipennis*	E	no	*N. cruentatus* seems better at high prey densities but *C. jorgepastori* seems better at low prey densities	not clear	main biocontrols both exotic
Moraes et al. 1998	3	*Anticarsia gemmatalis*	E	no	not explicit, but predators may be agents of NPV dispersal	not studied but viable NPV may be excreted in predators' feces	
Nakai & Kunimi 1998	2	*Adoxophyes* sp.	E	no	not explicit	parasitoid development delayed in diseased larvae	
Pfannenstiel & Yeargan 1998	6	unspecified	E	no	suggest designer polycultures may attract complementary predators	differential selectivity for different crops at a small scale by hemipterans	
Poprawski et al. 1998	3	*Bemisia argentifolii*	E	no	*P. fumosoroseus* & *S. parcesetosum* feasible, *B. bassiana* & *S. parcesetosum* questionable	lack of IGP & IGP, respectively	
Rutledge & Wiedenmann 1999	3	various stemborers	E	no	none	scale-dependent habitat partitioning - preferences for plant volatiles	
Sands & Coombs 1999	3	*Nezara viridula*	E	no	*T. giacomellii* deemed sufficiently specific to introduce	lack of potential IGP	
Schausberger & Croft 1999a	13	*Tetranychus urticae*	E	no	no tactical recommendation found	immature predators showed different "profiles;" some could	

						avoid IGP	
Schausberger & Croft 1999b	13	*Tetranychus urticae*	E	no	no tactical recommendation found	more heterospecific predation in generalists more cannibalism in specialists	
Schoenly et al. 1998	≥88	unspecified -- many	O	no	biocontrol in this system involves many spp. at multiple trophic levels	undetermined	
Sivinski et al. 1998	3	dipterans, particularly *Anastrepha ludens*	E	no	context-dependent	some IGP	
Slone & Croft 1998	4	*Panonychus ulmi* & *Tetranychus urticae*	E	yes	not explicit-but Zetzillia mali may displace T. pyri	IGP & contact avoidance	
Snyder & Wise 1999	≥14	seven different insects	E	no	guild augmentation improved control in some crops, but not in others	interference, and IGP on lycosids strongly suspected	
Stark et al. 1999	2	*Harrisina brillians*	E	no	unclear if both spp. are needed, but they do seem compatible	parasitoid prefers healthy hosts over those infected with HbGV	spatial hetero-geneity may be important for coexistenc e
Valladares & Salvo 1999	49	*Liriomyza huidobrensis*	E	no	diversity in native habitat can assist biocontrol in cultivated areas	weak interactors in native habitat can be strong interactors in cultivation	

Wei et al. 1998	6	*Archips argyrospila*	O	no	not explicit	habitat partitioning by host stage attacked	
Wells & McPherson 1999	5	*Myzus nicotianae*	O	no	none	*Coccinella septempunctata* & *Harmonia axyridis* show different seasonal patterns	

Citation comparing multiple biocontrol agents to pick one as the most promising	**Number of natural enemies**	**Most promising biocontrol agent**	**Pest species**
Grafton-Cardwell et al. 1999	4	*Ipheseius degenerans*	*Scirtothrips citri*
Horgan et al. 1999	11	*Cyzenis albicans*	*Operophtera brumata*
McGregor et al. 1998	3	*Trichogramma minutum*	*Choristoneura rosaceana*
Parry et al. 1998	2	*Podisus brevispinus*	*Malacosoma disstria*
Sivinski et al. 1998	2	context-dependent	*Anastrepha suspensa*

Citation examining multiple natural enemies that provide biocontrol	**Number of natural enemies**	**Pest species**	**Survey?**	**Nonspecific habitat modification?**
Anderson & Yeargan 1998	6	*Helicoverpa zea*		planting date & spacing
Argov & Rossler 1998	6	*Phyllocnistis citrella*		
Ballal & Singh 1999	3	unspecified		
Bigger & Chaney 1998	≥7	*Brassica* pest complex		intercropping
Boyd & Boethel 1998	3	soybean pest complex		
Brewer et al. 1998	2	*Diuraphis noxia*		
Brownbridge et al. 1999	10	*Taeniothrips inconsequens*	yes	
Bruck & Lewis 1998	8	*Ostrinia nubilalis*		

Carlson et al. 1999	2	*Musca domestica*		
Crespo et al. 1998	2	*Musca domestica*		
Degooyer et al. 1999	5	*Empoasca fabae, Hypera postica*		intercropping
Dry et al. 1999	5	*Musca domestica*		
French et al. 1998	73	unspecified		no-tillage planting
Gaasch et al. 1998	≥22	unspecified		
Geden et al. 1998	3	*Musca domestica*		
Geervliet et al. 1998	2	*Pieris rapae*		insecticide
Gerling & Narango 1998	5	*Bemisia tabaci*		
Gonzalez-Hernandez et al. 1999	5	*Dysmicoccus brevipes*		
Goolsby et al. 1998	≥11	*Bemisia tabaci*		
Greenberg et al. 1998	2	various Lepidoptera		
Hatting et al. 1999	8	aphids, particularly *Diuraphis noxia*	yes	
Heinz & Parrella 1998	5	*Bemisia argentifolii*		
Heinz 1998	2	*Myzus persicae & Aphis gossypii*		
James et al. 1999	33	various scale insects		presence/absence of ants
Jewett & Carpenter 1999	2	*Helicoverpa* spp., *Heliothis* spp.		
Jones et al. 1998	2	*Bemisia argentifolii*		
Liebhold et al. 1998	4	*Lymantria dispar*		
Lopez et al. 1999	10	*Anastrepha* spp.	yes	
McCravy & Berisford 1998	3	*Rhyacionia frustrana*		
Meagher et al. 1998	≥14	*Eoreuma loftini & Diatraea saccharalis*	yes	
Morrill et al. 1998	2	*Cephus cinctus*		
Nabli et al. 1999	≥8	unspecified		intercropping
Ogol et al. 1998	10	stem boring Lepidoptera		
Prasifka et al. 1999	≥15	cotton pest complex		adjacent sorghum

Riudavets & Castane 1998	18	*Frankliniella occidentalis*	yes	
Rothwell & Smitley 1999	≥10	*Ataenius spretulus*		golf course maintenance
Roy et al. 1999	≥12	*Tetranychus mcdanieli*		cropping & pesticide regime
Silva et al. 1999	5	none specified		
Smitley et al. 1998	≥7	*Ataenius spretulus* & *Aphodius granarius*		golf course maintenance
Suenaga & Hamamura 1998	24	*Plutella xylostella*		
Taylor & Szalanski 1999	5	unspecified Diptera		
Taylor et al. 1998	13	*Musca domestica*		
Tipping et al. 1999	2	*Leptinotarsa decemlineata*		
Weseloh 1998	2	*Lymantria dispar*		
Wilson-Rummenie et al. 1999	≥30	*Nala lividipes*, *Agrypnus variabilis* & *Cestrinus trivialis*		tillage regime
Wunderlich & Giles. 1999	3	none specified		

Appendix C. Latin names and natural history of species studied.

Common name	**Scientific name (if known)**	**Natural history**
pea aphid	*Acyrthosiphon pisum*	herbivore
thrips	mostly *Frankliniella occidentalis*	herbivore
bean aphid	*Aphis fabae*	herbivore
green peach aphid	*Myzus persicae*	herbivore
transient aphids	Aphididae	herbivore
whiteflies	mostly *Trialeurodes vaporariorum*	herbivore
spotted cucumber beetle	*Diabrotica undecimpunctata*	herbivore
plant bugs	*Lygus* sp.	herbivore
pea leaf weevil	*Sitona lineatus*	herbivore
unidentified mites	Acari	herbivore
unidentified leafhoppers	Cicadellidae	herbivore
unidentified caterpillars	Lepidoptera	herbivore
unidentified slugs	Stylommatophora	herbivore
damsel bug	*Nabis alternatus*	predator
big-eyed bug	*Geocoris* sp.	predator
minute pirate bug	*Orius tristicolor*	predator
banded-wing thrips	unidentified Aeolothripidae	predator
green lacewing	*Chrysoperla plorabunda*	predatory larvae, adults feed on pollen
green lacewing	*Chrysopa* sp.	predator
brown lacewing	unidentified Hemerobiidae	predator
seven-spotted ladybird beetle	*Coccinella septempunctata*	predator
eleven-spotted ladybird beetle	*Coccinella undecimpunctata*	predator
multicolored Asian ladybird beetle	*Harmonia axyridis*	predator
convergent ladybird beetle	*Hippodamia convergens*	predator
two-spotted ladybird beetle	*Adalia bipunctata*	predator
ladybird beetle	*Cycloneda pollita*	predator
ground beetle	*Pterostichus melanarius*	predator
ground beetle	*Amara* sp.	predator
ground beetle	*Bembidion* sp.	predator
predaceous gall midge	*Aphidoletes aphidimyza*	predatory larvae
hoverflies	unidentified Syrphidae	predatory larvae, adults feed on nectar and pollen

ant	*Myrmica* sp.	omnivore
ant	*Lasius* sp.	omnivore
parasitoid wasp	*Aphidius ervi*	parasitoid
parasitoid wasp	*Aphidius* sp.	parasitoid
parasitoid wasp	*Praon* sp.	parasitoid
hyperparasitoid	unidentified Hymenoptera	hyperparasitoid
hunting wasp	*Pemphredon* sp.	predator
hunting wasp	*Psenulus* sp.	predator
hunting wasp	*Diodontus* sp.	predator
harvestman	*Phalangium opilio*	detritivore/predator
dwarf spider	*Erigone* sp. or spp.	predator
orb weaver spider	*Zygiella* sp.	predator
orb weaver spider	*Tetragnatha laboriosa*	predator
spider	*Araneus diadematus*	predator
spider	*Lepthyphantes tenuis*	predator
spider	*Theridion bimaculatum*	predator
jumping spider	unidentified Salticidae	predator
wolf spider	unidentified Lycosidae	predator
centipede	unidentified Chilopoda	predator
pea aphid fungal pathogen	*Pandora neoaphidis*	pathogen
pea aphid fungal pathogen	*Entomophthora chromaphidis*	pathogen
earwig	*Forficula auricularia*	detritivore/predator
springtails	unidentified Collembola	detritivore
earthworms	unidentified Oligochaeta	detritivore
frog		transient
killdeer		transient
crow		transient
sparrow		transient
cat		transient
dog		transient
rabbit		transient
deer		transient

Appendix D. Pearson correlation coefficient matrix for abundant taxa in Sumner and Fife pea plots, 1997-1999 at different scales. Plant scale correlation coefficients were calculated from data from

Plant scale	Leaves	Pea aphids	Thrips	Bean aphids	Other aphids	Whiteflies	Cadavers	Parasitoids	Mummies	Syrphid eggs	Syrphid larvae	Syrphid pupae	Spiders	Coccinellids
Leaves	1.00													
Pea aphids	0.26*	1.00												
Thrips	0.41*	-0.03	1.00											
Bean aphids	0.07	0.07	-0.02	1.00										
Other aphids	0.24*	0.03	0.15*	0.00	1.00									
Whiteflies	0.37*	0.07	0.21*	-0.01	0.15*	1.00								
Cadavers	0.13*	0.46*	-0.09*	0.09	-0.02	0.03	1.00							
Parasitoids	0.07	-0.01	0.02	-0.02	0.00	-0.02	-0.02	1.00						
Mummies	0.17*	0.26*	-0.05	0.02	0.01	0.02	0.34*	-0.02	1.00					
Syrphid eggs	0.09	0.17*	0.04	-0.03	-0.02	0.08	0.00	0.02	0.04	1.00				
Syrphid larvae	0.28*	0.11*	0.16*	-0.02	0.09	0.19*	0.04	-0.02	0.07	0.08	1.00			
Syrphid pupae	0.14*	-0.02	0.10*	-0.01	0.11*	0.08	-0.02	0.08	0.01	-0.01	0.14*	1.00		
Spiders	0.15*	-0.02	0.22*	-0.01	0.03	-0.05	-0.05	0.01	-0.03	-0.03	0.06	0.04	1.00	
Coccinellids	0.04	0.10*	0.00	-0.01	0.01	0.00	0.18*	-0.01	0.04	-0.01	-0.02	-0.01	0.04	1.00

*Represents statistically significant correlation after Bonferroni correction for multiple comparisons.

Plot scale	Leaves	Pea aphids	Thrips	Bean aphids	Other aphids	Whiteflies	Cadavers	Parasitoids	Mummies	Syrphid eggs	Syrphid larvae	Syrphid pupae	Spiders	Coccinellids
Leaves	1.00													
Pea aphids	0.28*	1.00												
Thrips	0.54*	-0.13	1.00											
Bean aphids	0.16	0.16	-0.13	1.00										
Other aphids	0.33*	-0.10	0.28*	0.03	1.00									
Whiteflies	0.53*	0.10	0.46*	0.06	0.24*	1.00								
Cadavers	0.24*	0.68*	-0.12	0.23	-0.05	0.06	1.00							
Parasitoids	0.14	-0.04	0.07	-0.04	0.01	-0.04	-0.06	1.00						
Mummies	0.33*	0.52*	-0.07	0.25*	0.15	0.03	0.68*	-0.01	1.00					
Syrphid eggs	0.16	0.21	0.01	-0.08	-0.03	0.09	-0.02	-0.04	-0.01	1.00				
Syrphid larvae	0.44*	0.29*	0.31*	0.06	0.20	0.30*	0.10	0.10	0.10	0.09	1.00			
Syrphid pupae	0.28*	-0.06	0.35*	-0.06	0.09	0.44*	-0.05	0.04	-0.05	0.01	0.25*	1.00		
Spiders	0.27*	-0.14	0.44*	-0.05	0.04	-0.05	-0.12	0.07	-0.12	-0.05	0.18	-0.02	1.00	
Coccinellids	0.14	0.34*	-0.06	0.09	0.01	0.15	0.59*	-0.01	0.40*	-0.01	-0.03	0.04	-0.02	1.00

*Represents statistically significant correlation after Bonferroni correction for multiple comparisons.

Farm scale	Leaves	Pea aphids	Thrips	Bean aphids	Other aphids	Whiteflies	Cadavers	Parasitoids	Mummies	Syrphid eggs	Syrphid larvae	Syrphid pupae	Spiders	Coccinellids
Leaves	1.00													
Pea aphids	0.44	1.00												
Thrips	0.55	-0.24	1.00											
Bean aphids	0.45	0.55	-0.22	1.00										
Other aphids	0.56*	-0.02	0.46	-0.09	1.00									
Whiteflies	0.66*	0.12	0.56*	0.02	0.68*	1.00								
Cadavers	0.42	0.81*	-0.19	0.64*	-0.10	0.10	1.00							
Parasitoids	0.12	-0.19	0.24	-0.23	0.27	0.12	-0.24	1.00						
Mummies	0.46	0.78*	-0.10	0.53	-0.07	0.08	0.89*	-0.13	1.00					
Syrphid eggs	0.10	0.12	0.08	-0.23	0.26	0.17	-0.19	0.02	-0.04	1.00				
Syrphid larvae	0.70*	0.46	0.27	0.48	0.55	0.47	0.28	0.06	0.27	0.20	1.00			
Syrphid pupae	0.42	-0.17	0.59*	-0.15	0.34	0.69*	-0.14	0.08	-0.14	0.10	0.27	1.00		
Spiders	0.32	-0.17	0.55	0.07	0.08	-0.15	-0.14	0.07	-0.12	-0.04	0.21	0.09	1.00	
Coccinellids	0.15	0.35	-0.09	0.31	-0.08	0.08	0.60*	-0.09	0.63*	0.02	-0.07	-0.04	-0.14	1.00

*Represents statistically significant correlation after Bonferroni correction for multiple comparisons.

Appendix E. A mathematical model of the effect of intraguild predation on aphid control in an annual system.

Introduction

The impact of natural enemies on prey populations is highly variable. While some species have been decimated by disease or predation, others seem to flourish despite the action of natural enemies (Hawkins et al. 1997). This contrast is evident in the varied outcomes of biological control programs, which seek to control pests by using natural enemies. A recent review found that for classical biological control programs, 16% of targeted pests have been completely controlled, while 40% were partially controlled, and 44% were not at all controlled (U. S. Congress 1995).

While these programs may fail for several reasons, intraguild predation (IGP) has recently been heavily scrutinized as a mechanism disrupting biological control (Rosenheim et al. 1995). IGP occurs when an organism eats a potential competitor (Polis and Holt 1992). Biological control workers should be concerned when IGP is observed between biological control agents, because it has disrupted pest control in some settings (Rosenheim et al. 1993). Indeed, it is possible that biological control efforts can be counterproductive when an IG predator is introduced where IG prey already suppress the pest to some degree.

Rosenheim et al. (1995) conducted an extensive review of several mathematical models of biological control that include IGP. Two groups of models were identified: (1) detailed, empirically-based simulations of specific systems, and (2) general analytical models of IGP. The simulations suggested that adding IG predator to incumbent natural enemies can either improve or disrupt biological control. The analytical models developed for IGP among pathogens and parasitoids also found that biocontrol could be improved or disrupted by the addition of an IG "predator" (in the broad sense, which includes pathogens and parasitoids that always kill their competitors when they occupy the same individual host, whether by strict IGP or by superior exploitation of the host). Interestingly, models based on predators consistently found that IGP disrupts biocontrol. This difference may be because IGP among parasitoids and pathogens generally occurs in or on a shared host individual, which is killed along with the IG victim, while IGP among predators need not result in mortality of the shared prey.

An example of the analytical models can be found in Hassell's (1978) seminal monograph. Hassell describes a 3-equation model of two parasitoid species and one prey species that includes asymmetric IGP. The IGP is asymmetric because one parasitoid always eliminates the other when both are found in a multiply-parasitized host. Analysis of the model was primarily concerned with classical biocontrol and the question of whether it is better to introduce one or two (or more) species of biocontrol agents. The stability of the model was analyzed, and a range of outcomes was found. For some parameter combinations, only one parasitoid can coexist with the prey, while others allow the three species to coexist in a locally stable equilibrium. In this model, the stable coexistence of three species is promoted by high efficiency and aggregation of the parasitoids. These traits also promote lower host populations at equilibrium. Stable three-species coexistence becomes more likely if the IG victim has a greater search rate than the IG predator.

Polis et al. (1989) presented three general analytical models of IGP based on predators in the strict sense (not including parasitoids and pathogens). The first was produced by modifying the Lotka-Volterra model of competition. This was accomplished by adding a one-way IG interaction, in which predator *A* consumes IG prey *B*, but *B* does not consume *A*. They then compared isoclines of the IGP model to isoclines from the Lotka-Volterra model. When *A* excludes *B* in the Lotka-Volterra model, the inclusion of IGP did not change the qualitative outcome. However, in other cases where the Lotka-Volterra model predicts coexistence, a priority effect, or *B* excluding *A*, the inclusion of IGP by *A* on *B* can tip the balance in favor of *A*. Thus, in the extreme case, where the Lotka-Volterra model predicts that *B* excludes *A*, sufficiently strong IGP by *A* on *B* can allow *A* to exclude *B*.

Next, Polis et al. (1989) modified the "pure exploitative" competition model developed by Schoener (1976). In the "pure exploitative" model, a fixed level of resource is divided among two species in competition, and neither species has an exclusive resource. Three key parameters determine which species is the superior exploitative competitor and excludes the other. These are (1) the relative likelihood of obtaining the shared resource, (2) the rate of energy input use of the two species, and (3) the density-independent maintenance and replacement cost of individuals. If the latter two parameters are equal for the two species, then the species with the greater likelihood of obtaining the shared resource excludes the other. The addition of one-way IGP (Polis et al. 1989) qualitatively changes the possible outcomes in this model. If the superior exploiter engages in IGP, then it remains as the species that excludes its competitor. However, IGP by the inferior exploiter yields a range of outcomes. The superior exploiter may still exclude its competitor, but the two species may also persist in a predator-prey-like interaction with damped oscillations. With sufficient IGP, the inferior exploiter may exclude the superior exploiter.

The third model of IGP in Polis et al. (1989) was a two-species model in which the IG predator also engaged in cannibalism. They found that for the IG prey to persist in this model, the impact of cannibalism on the IG predator must exceed the impact of IGP on the IG prey. The models developed by Polis et al. (1989) were two-equation models that did not include resource dynamics. However, the addition of a third equation for the limiting resource does not change their findings (Polis and Holt 1992).

Complex simulation models that include IGP have been developed for several systems by Gutierrez and collaborators in a series of papers (Gutierrez et al. 1984, Gutierrez et al. 1990, and Gutierrez 1992). These models are modular, with a separate equation for each species, and sometimes for each stage class. As many as 7 species have been modeled at once, at multiple trophic levels (plant, herbivores, and natural enemies). These models are biologically rich, with several parameters determined for each species, and often for different life stages of the same species. The modularity of the models allows for testing the consequences of IGP by adding or removing species involved in the interaction.

For example, Californian alfalfa is one system that was modeled. For the models in which IGP was investigated, the system consists of alfalfa, two species of aphid, and the natural enemies of the aphids. Damage to alfalfa from herbivores other than aphids was also included in these models, but will not longer be considered in this paper. An early set of simulations tested the effects of a parasitoid (IG victim) and a ladybird beetle (IG predator) on aphid populations (Gutierrez et al. 1984). They first simulated four possibilities:

(1) Alfalfa with aphid populations free from natural enemies. In this case, aphid populations cycle over time.

(2) Alfalfa, aphids, and the parasitoid. Parasitoids were introduced at low density, but quickly increased, which lowered aphid densities. The insect populations then appear to reach an equilibrium state.

(3) Alfalfa, aphids, and ladybird beetle. Aphid populations cycle, similarly to case 1, but with a larger amplitude. The average aphid population size over time is lower than in case 1, but higher than case 2.

(4) Alfalfa, aphids, the parasitoid, and the ladybird beetle. Again, aphid populations oscillate. Over time, the average aphid population size is lower than when the ladybird beetle is the only natural enemy in the system, but higher than when the parasitoid acts alone on aphids.

To summarize these results, aphid populations in case 2 < case 4 < case 3 < case 1. In other words, IGP by the ladybird beetle on the parasitoid disrupted aphid control, when compared to the parasitoid-only situation. In a fifth simulation, another IG predator, a green lacewing, was added to the species included in case 4. In this system, lacewing larvae attack all of the other insects and are attacked by only themselves (cannibalism). The addition of the lacewing displaced both of the other natural enemies and drove aphid populations to an equilibrium level that was lower than in any of the other simulations. While this theoretical result is promising from a biocontrol perspective, Gutierrez et al. (1984) note that it is not observed in field data. One possible factor contributing to this discrepancy is that alfalfa loses its attractiveness to green lacewings adults as it matures (Gutierrez et al. 1990).

Gutierrez et al. (1990) improved the original alfalfa model by modifying some of the functional response terms and incorporating a new module for a fungal pathogen that infects aphids. The simulations performed in this analysis included:

(1) Alfalfa with aphid populations free from natural enemies. [Although the species are the same in this simulation as in (1) from Gutierrez et al. 1984, the population dynamics are a qualitatively better fit to field data.]

(2) Alfalfa, aphids, and fungal pathogen.

(3) Alfalfa, aphids, and ladybird beetle.

(4) Alfalfa, aphids, pathogen, and ladybird beetle.

(5) Alfalfa, aphids, pathogen, ladybird beetle, and parasitoid.

The fifth case is the only one in which IGP occurs: ladybird beetles consume parasitoids, and the fungal pathogen acts as an IG predator when fungus and parasitoid share a host aphid. While IGP, particularly by the fungus, reduces the effectiveness of the parasitoid, it manages to persist in the system. Aphids numbers are lowest in case 5.

Further fine-tuning of this model to match field data (Gutierrez 1992) did not change the major finding above.

Rosenheim et al. (1995) caution that some of the simplifying assumptions in the alfalfa models are as yet unsupported. They were particularly concerned with the assumption that IG predator preferences are directly proportional to the abundance (in biomass) of each potential prey species, and that the greater biomass of herbivorous prey would lessen the impact of IGP in the models.

Schreiber and Gutierrez (1998) used a more general equilibrium analysis of a simplified multitrophic model to explore the consequences of IGP. In particular, they asked what conditions allow an IG prey species to invade a system that already contains an IG predator, a shared prey species, and a plant. In their model, this could only occur when the IG prey's superiority in exploitative competition outweighs the impact of IGP. This result is consistent with those of Polis et al. (1989) and Polis and Holt (1992).

An assumption of many of the models reviewed by Rosenheim et al. (1995) is that IG predators do not discriminate among prey, so herbivores and IG prey are taken in proportion to their abundance (measured in biomass). However, IG predators can discriminate among prey, and this can affect the dynamics of the system. For example, Kindlmann and Ruzicka (1992) developed a simulation model based on empirical results from field studies in cages of an aphid system. The aphids were attacked by a parasitoid *(Diaeretiella rapae)* in some cages and by the parasitoid and a predator *(Metasyrphus corollas)* in others. In the cages where both the predator and the parasitoid were present, aphid populations were lower and the percentage of aphids parasitized was higher. Kindlmann and Ruzicka used their model to show that these population-level patterns could be explained by the predator's preference for unparasitized aphids over parasitized aphids (documented in the laboratory by Ruzicka [1976]). They suggested that field observations of high percentage parasitism might sometimes indicate a strong effect of predators rather than high parasitoid efficiency.

The timing of IGP is crucial to whether it disrupts biological control. While it is easier to observe IGP under laboratory conditions where species are confined in an enclosed arena, such observations do not necessarily indicate that disruption (or even IGP) would occur in the field. Obviously, IGP that occurs after harvesting in an annual agroecosystem may not matter to pest control, especially if insect dynamics from season-to-season are only loosely connected. (While obvious, this scenario has apparently been forgotten in the literature.)

A more interesting possibility is that IGP might improve biological control if IG prey subsidize an IG predator. This subsidy could be particularly important in allowing predators to persist while prey are scarce, such as early in the growing season – again, the timing of IGP may be important. The role of cannibalism (a special case of IGP) in allowing persistence of predators during prey shortages has been demonstrated in laboratory settings (Fox 1975). A field example of the importance of early-season events comes from Indonesian rice, where biological control by generalist predators is improved when they have alternative prey early in the growing season (Settle et al. 1996). However, in the rice example, the alternative prey were mostly detritivores, not IG prey.

Previous models of IGP and biological control may have overlooked the possibility of beneficial early-season consequences of IGP because they have emphasized finding the conditions that permit IG predators and IG prey to coexist. The mathematical model presented in this chapter emphasizes single season dynamics. This model is combined with data from fieldwork conducted in an annual crop system – peas in western Washington. In this system the answer to the longer-term question of coexistence depends on landscape and weather, and are beyond the scope of this model.

The life history traits of biocontrol agents that are most desirable in relatively permanent systems, such as forests, may not be the same in highly disturbed annual systems (Ehler and Miller 1978, Hassell 1978, Wissinger 1997). Ehler and Miller (1978) used "r- and K- selection" theory to help determine the desirable attributes of biocontrol agents in different systems. Species with relatively high reproductive potential and superior dispersal ability, but with lower competitive ability, are considered "r-selected." They are predicted to be numerically dominant in highly disturbed systems such as annual crops. Therefore, Ehler and Miller suggested that "r-selected" natural enemies would be more effective biocontrol agents in annual crops. This suggestion was supported with data showing that a complex of polyphagous predators was primarily responsible for controlling cotton pests in California. A group of parasitoids was present in the cotton, at lower density than the predators, and was less important for controlling pests. The predators were considered "r-selected," while the parasitoids were not.

Ehler and Miller (1978) did not mention whether they observed IGP in the cotton system. However, when predators and parasitoids share the same prey, asymmetrical IGP often occurs, in which the predators eat parasitoids (Rosenheim et al. 1995). This IGP may contribute to the early-season abundance of predators, and temporarily improve pest control. This possibility is explored in the model below.

The model

The model consists of three ordinary differential equations. First, I describe the population dynamics of pea aphids (denoted by V) as growing exponentially at a rate, r, minus mortality (m) from two predator species, P and Q, at rates of $m_{P.V}$ and $m_{Q.V}$, respectively.

$$\frac{\mathrm{d}V}{\mathrm{d}t} = rV - m_{P.V}PV - m_{Q.V}QV \qquad \text{Eq. 1}$$

Next, I assume that predator species P is always the victim of intraguild predation, and that predator Q is always responsible for intraguild predation at a rate $m_{Q.P}$. In addition, I assume that both predators leave the area at a constant rate, E, while they are both drawn into the area as a function of prey density. In the case of P, it only responds to pea aphids:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{i_P V}{s_P + V} - E_P P - m_{Q.P}QP \qquad \text{Eq. 2}$$

The positive term is a saturating recruitment curve, such that more of species P arrives in the area per unit time as pea aphid density (V) increases. The parameter i in this term defines the asymptotic rate of natural enemy arrival as V approaches infinity, while s establishes the number of prey at which the enemy arrival rate is half of its maximum. Because predator Q attacks both pea aphids and predator P, I describe its arrival as a function of the sum of $V + P$, with the response of Q to P proportional to the relative attack rates of Q against V and P ($m_{Q.V}$ and $m_{Q.P}$, respectively):

$$\frac{dQ}{dt} = \frac{i_Q\left[V + \left(m_{Q.P} / m_{Q.V}\right)P\right]}{s_Q + V + \left(m_{Q.P} / m_{Q.V}\right)P} - E_Q Q \qquad \text{Eq. 3}$$

Because analytical results were difficult to obtain, I numerically simulated the model across a variety of parameter values (Table E.1). The timestep I chose was one-tenth of a day, and a single season (61 days) was the duration of each simulation. I used field data from 1997-1999 as well as values in the literature to parameterize the model and set initial conditions.

To approximate the initial number of predators and pea aphids to use in the model, I assessed the density of these taxa during the first sample that I took at each site in each field season. Because I used plots of different sizes in each of my field seasons, I take the density per plant and multiply that by 500 to obtain the initial conditions within a plot of 500 peas (which would occupy an area of roughly 2 m × 5 m following my planting scheme and corresponds with the plots I planted in Sumner in 1999). The initial numbers of pea aphid alates (winged adults, which are the initial aphid colonists at the beginning of the growing season) and other arthropods varied greatly from year-to-year, from site-to-site, and from plot-to-plot within sites and years (Table E.2). The factors that determine initial population sizes are often found beyond the field. For example, while I observed some pea aphids overwintering as eggs on weeds at the Fife and Sumner sites, most of the pea aphids alates that settle on sprouting pea plants appeared to originate from areas beyond the site boundaries. The same applies to most of the natural enemies found early in the season. Some natural enemies do not arrive in the field for several weeks after peas are planted. The longest delay in arrival was observed with the various hunting wasps (Chapter 2).

The rate of reproduction (*r*) for pea aphids has been measured by Campbell (1926) and roughly equals 0.04. In the field, *r* will vary with plant quality, abiotic conditions, and probably even with predator activity, but for now, I will ignore these complications.

Natural enemies showed considerable interspecific variation in kill rate. I extrapolated parameter estimates for the mortality that each natural enemy taxon from my direct behavioral observations, which provide the rate at which an individual predator kills pea aphids. I converted the rate per minute into a rate per one-tenth of a day (the duration of the timestep I chose for the simulation). If I assume that this rate holds across the variety of aphid densities seen during the season, then it can be divided by the average number of pea aphids per plot observed over all of my data (roughly equal to 1,000). The result is a crude estimate of *m*, but captures the variation seen in the field (Table E.3).

The parameters relating to predator immigration and emigration are more difficult to obtain directly from my data. However, I can suggest reasonable values on the basis of many hours spent in the field. The parameter *E* roughly corresponds to the turnover of predators during each timestep, or more specifically, the percentage of the predator population that departs during each timestep. Thus, for mobile predators such as adult ladybird beetles, setting *E* equal to 0.5 is defensible (half of the adult ladybird beetles in a plot depart in 2.4 hours). Other predators, such as syrphid maggots, are much less mobile, but even these will depart from a plot given enough time, and setting $E = 0.05$ seems reasonable. Again, while many environmental factors will cause E to change in the field, for the purposes of my simulation, I treat E as a constant.

Parameters i and s are less straight-forward, but can still be presented in empirical terms by relating combinations of i and s to the resulting influx of predators when the density of pea aphids is held steady at 1 and at 40 per plant (Table E.4). When pea aphids reach the high density of 40 per plant, a 500-plant plot contains 20,000 aphids, and it would not be surprising if a dozen individual predators were to arrive in 2.4 hours, while at the low density, the number of arrivals should be lower. Of the combinations in Table E.4, the third one probably best reflects the typical case for my system, as it is uncommon to find many predators in a plot with such a low aphid density (Figure E.1).

Finally, the rate of intraguild predation must be assessed. When all trophic events are pooled over 1997-1999, less than 10% of them involved a predator eating another predator (6 out of 79 observations). A roughly similar fraction of all individuals counted in samples during the same period are predators or other natural enemies (2,484 out of 25,900). Thus, if I use these pooled data to represent the rate of intraguild predation ($m_{Q.P}$) in the model and apply the same procedure with which I obtained the estimate of m for various predators against pea aphids, then $m_{Q.P} \cong 0.014$. Although this suggests that predators will kill each other at a rate that is disproportionate to their contribution to the total number of individuals, this difference is not statistically significant (Chapter 2).

Simulation results and discussion

For most of the parameter combinations explored through simulation, IGP decreases the net effect of predators (Figure E.2). Therefore, IGP seems to hinder pest control more than it helps. However, under certain conditions, IGP improves control (Figure E.3a). This occurs when the initial number of aphids is low. This echoes results from a model of generalists natural enemies for biological control (Chang and Kareiva 1999). IGP allows the IG predator to increase in density prior to pest build-up and improve control through preventing an outbreak from occurring. However, this is a short-lived effect (Figure E.3b) if the pests manage to increase while IG prey density is low. Then, the depression of IG prey offsets the increase in IG predators, and IGP begins to decrease pest control.

Despite the interference between natural enemies, augmentation of an IG predator usually improves biological control in the simulations (for example, Figure E.2), albeit not by as much as augmentation of predators that do not engage in IGP. Augmentation by IG predators does disrupt control when the initial number of IG prey is relatively high (Figure E.4).

Limited sensitivity analysis of this model suggests that aphid load (pest suppression) is most affected by changes in the rate that IG prey attack the pest, and then by the rate at which IG predators attack the pest. While the rate of IGP (IG predators attacking IG prey) does affect pest suppression, it is the least influential rate (Figure E.5).

To date, analysis of this model has been accomplished through simulations that primarily focus on the tradeoff between the two natural enemy species at varying levels of IGP. While the model allows for additional complications, such as altering the relative attack rates of the two natural enemies against their shared prey, I have not yet performed such simulations. A general analytical solution to this model might be possible and would be desirable, but I have been unable to produce one.

A limitation of this model is that it neglects space and instead assumes that aphids and their natural enemies are evenly distributed on plants. However, pea aphids are patchily distributed in the field, and furthermore, their spatial distribution is affected by predator augmentation (Chapter 3). Plots in which tethered ladybird beetles were released had significantly lower plant-to-plant variation in pea aphid density than control plots, although the average pea aphid densities in the plots were not significantly different. Because the relationship between plant damage and pea aphid density is nonlinear (Yencho et al. 1985), spatial distribution of pea aphids may be an important consideration in their control. A spatially-explicit version of this model would be useful for addressing this matter.

The results of this model generally support increasing natural enemy populations, even if IGP occurs. This should be particularly encouraging for practitioners of conservation biological control. The premise of conservation biological control is that by making agroecosystems more favorable for resident natural enemies, pests con be more effectively suppressed (Barbosa 1998). In the context of this model, this premise holds unless the initial numbers of natural enemies (especially IG prey) are high and pests still remain at an undesirable level. Then, an alternative pest control tactic might be the introduction of a specialist natural enemy or a selective pesticide.

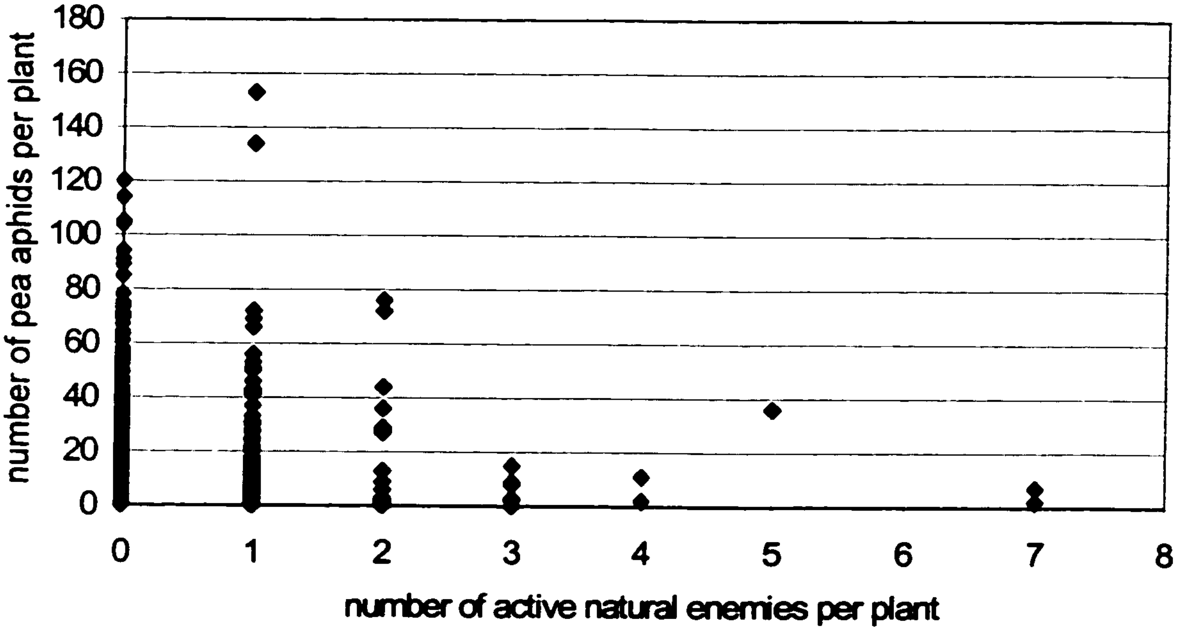


Figure E.1 Association of active predators and pea aphids, western Washington, 1997-1999.

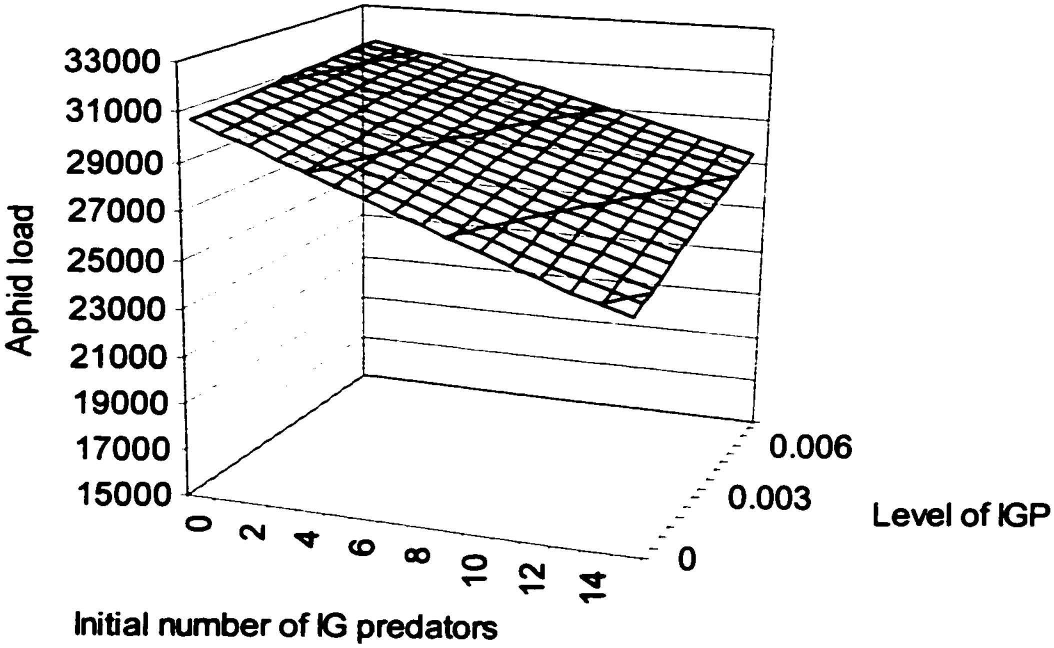
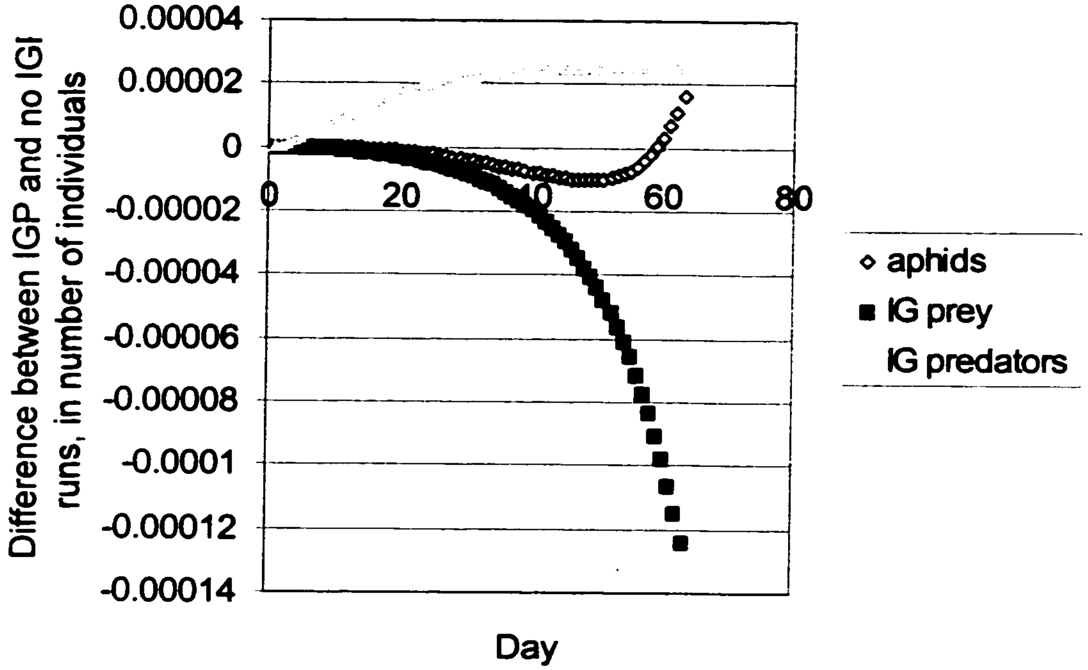


Figure E.2 Typical response of aphid load to changes in the level of intraguild predation and the initial number of intraguild predators. As IGP occurs more frequently, the net impact of the natural enemy guild decreases and thus the aphid load increases. However, the augmentation of an intraguild predator (represented in the model as an increase in initial number) still decreases aphid load. Initial aphid density equals 200 in the simulations that produced this graph.

a.


0.00004
0.00002
0
-0.00002
-0.00004
-0.00006
-0.00008
-0.0001
-0.00012
-0.00014
Difference between IGP and no IGI
runs, in number of individuals
0
20
40
60
80
Day
◇ aphids
■ IG prey
IG predators

b.

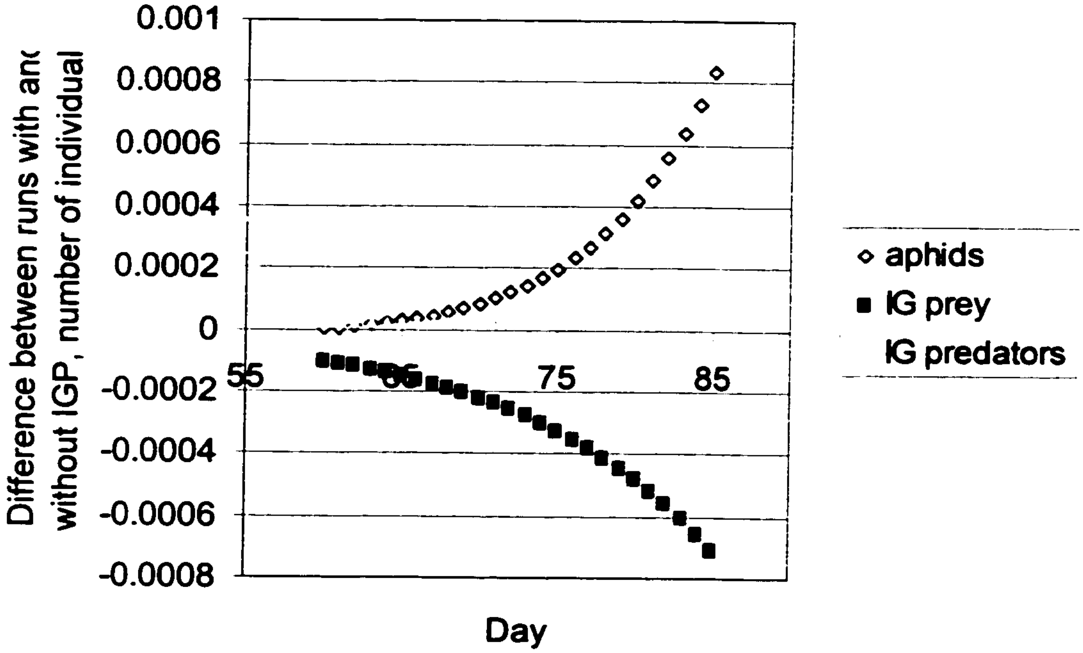

0.001
0.0008
0.0006
0.0004
0.0002
0
-0.0002
-0.0004
-0.0006
-0.0008
Difference between runs with anc
without IGP, number of individual
55
65
75
85
Day
◇ aphids
■ IG prey
IG predators

Figure E.3 An example of conditions where intraguild predation increases the net effect of two species of natural enemy on their shared prey. Initial conditions for these simulations were the same: 2 aphids, 0 intraguild prey, and 0 intraguild predators. Each data point is the difference between results from a simulation *with* IGP and a simulation *without* IGP. A positive value indicates that more individuals were produced in the simulation *with* IGP. Note that very early in the simulation, the number of aphids is lower in the simulation *with* IGP, due to the slight increase in the number of intraguild predators (figure 4.3a.). However, this changes with time, as the advantage in increased intraguild predators is offset by a greater decrease in the number of intraguild prey. Eventually, the number of aphids is higher in the simulation *with* IGP (figure 4.3b.)

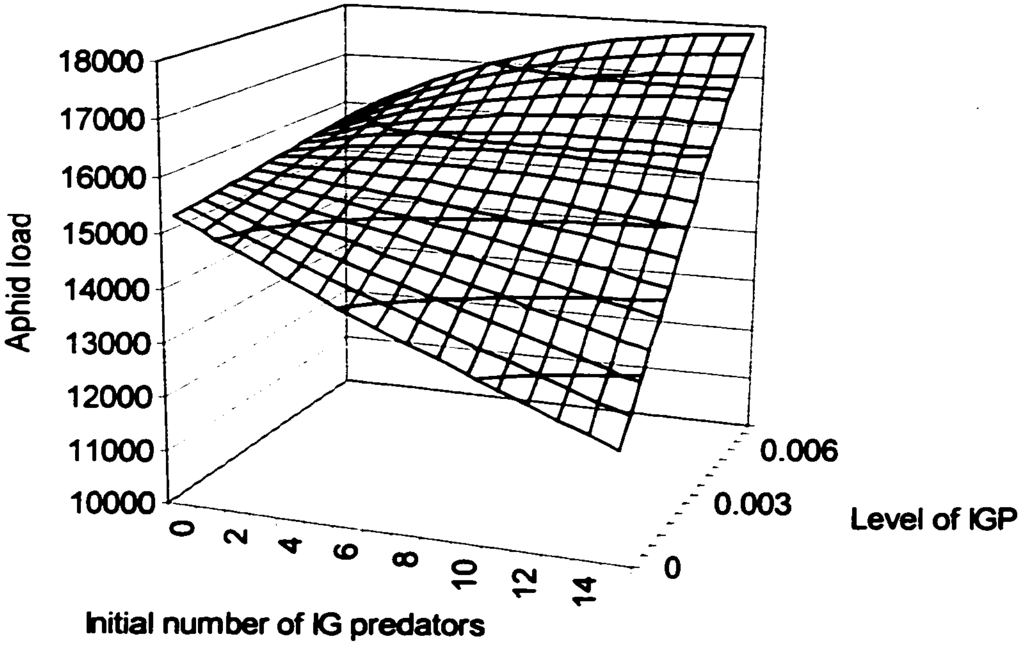


Figure E.4 Region where augmentation of an intraguild predator becomes counterproductive. The initial number of aphids equals 2 in these simulations. When compared to figure 4.1, note that at higher levels of IGP, increasing the initial number of intraguild predators causes an increase in the aphid load, rather than a decrease.

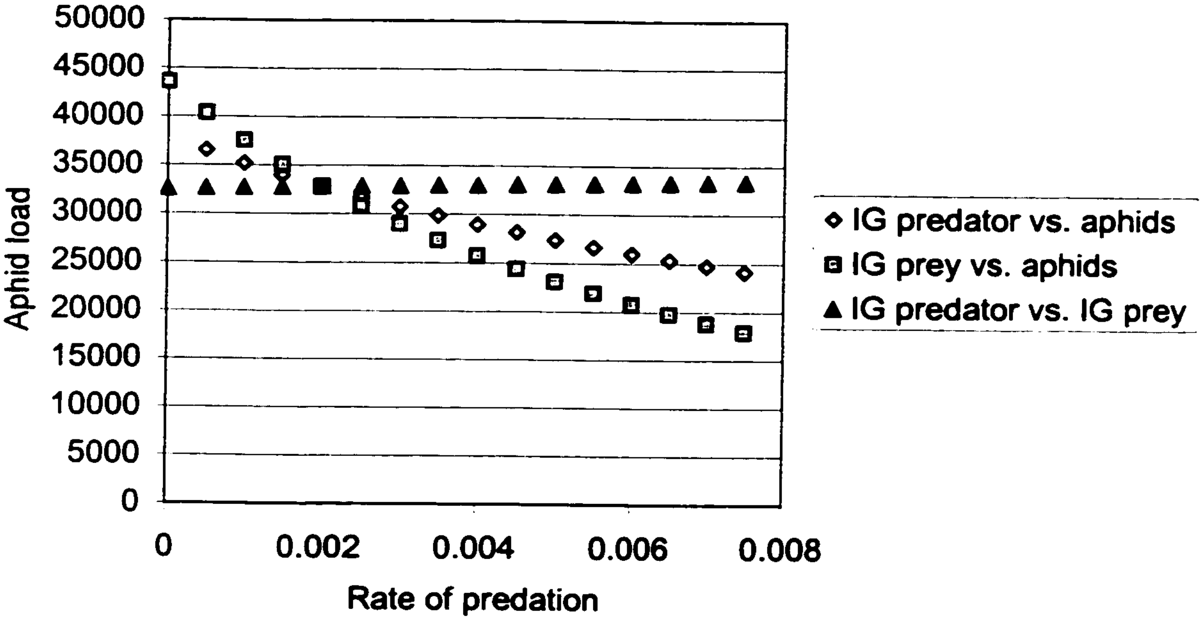


Figure E.5 Sensitivity analysis of the model to changes in different predation rates. In these simulations, parameters were held constant with the exception of a single predation rate in question. The response variable of aphid load changes the most when the attack rate of intraguild prey on aphids is changed. The model is least sensitive to changes in the rate of intraguild predation (intraguild predators attacking intraguild prey).

Table E.1 Parameter values and initial conditions used in simulations.

Parameter or initial condition	Values
Initial number of pea aphids, V (individuals)	2, 20, 200, 2000
Aphid reproduction, r (day^{-1})	0.04
Initial number of IG prey, P (individuals)	0 – 60
Initial number of IG predators, Q (individuals)	0 – 15
Pea aphid mortality from IG prey, $m_{P,V}$ (individuals^{-1}day^{-1})	0.002 – 0.004
Pea aphid mortality from IG predators, $m_{Q,V}$ (individuals^{-1}day^{-1})	0.002 – 0.004
IG prey mortality from IGP, $m_{Q,P}$ (individuals^{-1}day^{-1})	0 – 0.0075
Predator emigration, E (day^{-1})	0.1
Predator arrival term, i (day^{-1})	9000
Predator saturation term, s (individuals)	15000000

Table E.2 Variation in initial numbers of certain insects found in western Washington pea fields. Pea aphids are herbivorous insects that are consumed by parasitoids, syrphid larvae, and seven-spotted ladybird beetles. Seven-spotted ladybird beetles have been observed attacking syrphid larvae and developing parasitoids (contained within dead aphids).

Year	Site	Pea aphid alates	Parasitoids	Immature syrphids	Seven-spotted ladybird beetles
1998	Fife	0 - 0.125 per plant	0	0	0
1998	Sumner	0 - 0.4 per plant	0	0	0
1999	Fife	0 - 0.188 per plant	0	0 - 0.062 per plant	0 - 0.062 per plant
1999	Sumner	0.812 - 1.5 per plant	0	0 - 0.125 per plant	0 - 0.062 per plant

Table E.3 Estimates of m, aphid kill rate, for selected natural enemies of the pea aphid.

Natural enemy taxon (P, Q, etc.)	**Pea aphids killed per minute**	**Parameter estimate for $m_{P,V}$**
Hunting wasps	0.094	0.0135
Seven-spotted ladybird beetle	0.012	0.0017
Parasitoids	0.008	0.0012
Eleven-spotted ladybird beetle	0.005	0.0007
Immature syrphids	0.003	0.0004

Table E.4 Influx of predators for different combinations of i, s, and aphid density. Pea aphid densities between 1 and 40 per plant have been observed in the field.

Combination of i and s	Density of pea aphids	Resulting influx of predators
$i = 12, s = 150$	40 per plant	+ 11.9
	1 per plant	+ 9.2
$i = 15, s = 5000$	40 per plant	+ 12
	1 per plant	+ 1.4
$i = 9000, s = 15000000$	40 per plant	+ 12
	1 per plant	+ 0.3

Curriculum vitae

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Education

Ph.D., Department of Zoology, University of Washington, Seattle, WA, August, 2000. Peter Kareiva and Robert T. Paine, advisors. Dissertation title: Ecological interaction among natural enemies and its consequences for biological control.

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Publications

Schindler, D. E., G. C. Chang, S. Lubetkin, S. E. B. Abella and W. T. Edmondson. In press. Rare species in the phytoplankton community of Lake Washington.

Chang, G. C. and P. Kareiva. 1999. The case for generalists in biological control. In: *Theoretical Approaches to Biological Control.* B. Hawkins, ed., pp. 103-115. Cambridge University Press.

Chang, G. C. and A. R. Smith. 1999. Book review: "Phenotypic Evolution: a reaction norm perspective," by C. D. Schlichting & M. Pigliucci. *Animal Behaviour* 57: 1169-1170.

Chang, G. C. 1998. *Chrysoperla plorabunda* (Neuroptera: Chrysopidae) larvae feed disproportionately on thrips (Thysanoptera: Thripidae) in the field. *Canadian Entomologist* 130: 549-550.

Schultz, C. B. and G. C. Chang. 1998. Challenges in insect conservation: managing fluctating populations in disturbed habitats. In: *Conservation Biology: for the coming decade,* 2nd ed. P. L. Fiedler and P. M. Kareiva, eds, pp. 228-254. Chapman & Hall, San Francisco.

Chang, G.C. 1996. Comparison of single versus multiple species of generalist predators for biological control. *Environmental Entomology* **25**: 207-212.

Roberson, K. M., D. W. Edwards, G. C. Chang and C. N. Robertson. 1995. Isolation and characterization of a novel human prostatic stromal cell culture: DuK50. *In Vitro Cell. Dev. Biol. -- Animal* **31**: 840-845.

Polemics, J. [pseudonym for P. Klopfer, M. Buchanon, G. Chang, C. Gentzler, D. Hendricks, H. Naganna, M. Nealen, C. Osmun, A. Perez, N. Smith, S. Wu and G.

Young]. 1994. The postmodernist critique of science: is it useful? *Journal of the Elisha Mitchell Scientific Society* **110**: 113-120.

Fellowships and Grants

National Science Foundation Predoctoral Fellowship, 1994 – 1999.

Sigma Xi Grant in Aid of Research, $500, Spring 1999.

Oral Presentations at Scientific Meetings and Invited Seminars

Chang, G. C. 1999. The implications of habitat partitioning and intraguild predation for biological control of the pea aphid. University of Idaho / Washington State University joint course.

Chang, G. C. and B. Klepetka (listed alphabetically). 1999. Community ecology in agroecosystems. Tilth Producers (Washington) 1999 Conference.

Chang, G. C. 1999. Comparing the foraging behaviors of insect predators in an agroecosystem. Ecological Society of America Meeting.

Chang, G. C. 1995. An experimental study of the merits of single versus multiple species of generalist predators in biological control. Ecological Society of America Meeting.